Systematic Zoology

SOCIETY OF SYSTEMATIC ZOOLOGY

Taxonomic Methods, Their Bearing on Speciation	*R. A. Pimentel*	139
General Adaptation and Evolution	*W. L. Brown, Jr.*	157
Are There Rodent Suborders?	*A. E. Wood*	169
An Analysis of a Sample of Systematic Literature, 1758 to 1954	*D. L. Reish*	174
Points of View		
Problems of Higher Classification	*P. R. Ehrlich*	180
Similarity and Recency of Common Ancestry	*R. S. Bader*	184

THE UNIVERSITY OF MICHIGAN
DEC 29 1959
MUSEUMS LIBRARY

VOLUME 7 DECEMBER 1958 NUMBER 4

Systematic Zoology

LIBBIE H. HYMAN, *Editor pro tem*

Editorial Board

E. MAYR	1958	C. W. SABROSKY, *Chairman*
C. L. HUBBS	1959	L. H. HYMAN
I. M. NEWELL	1960	S. W. MULLER
B. PATTERSON	1961	H. H. ROSS

SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. Libbie H. Hyman, American Museum of Natural History, New York 24, New York.

Subscription rates are $4.00 to members, $7.00 to non-members and institutions. The price of single numbers, when available, is $1.50 to members and $2.00 to non-members. Annual dues are $1.00. Correspondence regarding subscriptions, purchases, non-receipt, and other non-editorial business should be addressed either to the secretary-treasurer, Dr. R. E. Blackwelder, Dept. of Zoology, Southern Illinois Univ., Carbondale, Ill., or to the acting treasurer, Dr. Joseph H. Camin, Dept. of Entomology, University of Kansas, Lawrence. Correspondence concerning membership and other aspects of the Society's affairs should be addressed to the secretary-treasurer, Dr. R. E. Blackwelder, Dept. of Zoology, Southern Illinois Univ., Carbondale, Ill.

The Society of Systematic Zoology

OFFICERS FOR 1958

President.....A. E. EMERSON
University of Chicago

President-Elect.....L. H. HYMAN
American Museum of Natural History

Secretary-Treasurer.....R. E. BLACKWELDER
Southern Illinois University

Acting Treasurer.....J. H. CAMIN
University of Kansas

THE COUNCIL

R. H. ARNETT, JR.	1958	W. I. FOLLETT
M. G. NETTING	1959	W. L. SCHMITT
W. H. BURT	1960	C. G. GOODCHILD
R. H. BAKER	1961	R. L. USINGER

Entered as second-class matter at the post office at Victor, New York, with an additional entry at Baltimore, Maryland.

THE SOCIETY OF SYSTEMATIC ZOOLOGY

Systematic Zoology

VOLUME 7, 1958

NUMBERS 1–4

ISSUED 1958, BALTIMORE, MD., U. S. A.

Systematic Zoology

PUBLISHED BY

THE SOCIETY OF SYSTEMATIC ZOOLOGY

Editor

LIBBIE H. HYMAN
American Museum of Natural History
New York City

Editorial Board

E. MAYR Harvard University	1958	C. W. SABROSKY, *Chairman* U. S. Dept. Agriculture
C. L. HUBBS Scripps Institute of Oceanography	1959	L. H. HYMAN American Museum of Natural History
I. M. NEWELL University of California, Riverside	1960	S. W. MULLER Stanford University
B. PATTERSON Harvard University	1961	H. H. ROSS Illinois Natural History Survey

The Society of Systematic Zoology

OFFICERS FOR 1958

President

A. E. EMERSON
University of Chicago

President-Elect

LIBBIE H. HYMAN
American Museum of Natural History

Secretary-Treasurer

R. E. BLACKWELDER
Southern Illinois University

Acting Treasurer

J. H. CAMIN
Chicago Academy of Sciences

THE COUNCIL

R. H. ARNETT, JR. St. John Fisher College	1958	W. I. FOLLETT California Academy of Sciences
M. G. NETTING Carnegie Museum	1959	W. L. SCHMITT United States National Museum
W. H. BURT University of Michigan	1960	C. G. GOODCHILD Emory University
R. H. BAKER University of Kansas	1961	R. L. USINGER University of California

Taxonomic Methods, Their Bearing on Subspeciation

RICHARD A. PIMENTEL

ALTHOUGH the subspecies has been severely criticized there seems to be sufficient reason to retain the concept. Subspeciation was and still is a logical extension of neo-Darwinian theory of species formation. Speciation mechanisms could result in once isolated, genetically divergent populations reuniting and, not having reached specific distinction, interbreeding. Also, populations at the above level of divergence could still be geographically isolated from one another. Both kinds of populations have been called subspecies, and there seems to be no reason to discontinue the practice. Although the basic microevolution theory has not been seriously attacked, critics of subspeciation have emphasized many weaknesses in conclusions inferred from theory. Throughout the original development and present opposition little attention has been given to taxonomic methods. The present paper considers the possible influence of taxonomic methods on characterizations of subspeciation and why most methods are generally valid but frequently unreliable. Also, there is an attempt to provide more exacting approaches to taxonomic studies by considering the importance of reliable techniques and giving procedures for ascertaining the degree of difference among populations. It is believed that until methodology is eliminated as a possible factor in this debate no concrete extension of theory is possible.

The issues against the subspecies can not be taken lightly. Dissatisfaction has led to studies reevaluating some subspecies. These reexaminations seem to indicate that subspecies display different geographical distributions depending upon the morphological characters used. As a result of these findings, the trinomen has been attacked and subspecies are considered subjective, mere matters of definition. The strongest objection is the discordance of characters. But, do subspecies really have different geographic distributions depending upon the morphological characters used? The author is convinced that these findings could have resulted from methods of study rather than conditions in nature. On the other hand character discordance might truly exist because of different rates of gene flow between once isolated populations, i.e., subspecies. This means of course that subspecies may rapidly assume the appearance of clines and perhaps should be considered as such. Also, certain aspects of population genetics might rapidly and completely obscure the picture of subspecies. If either be the case and subspecies in the old sense are rarities, the entire complex should be unraveled prior to deciding which do and which do not exist. The second emphasized objection is against the trinomen and its subjectivity of application. It does appear that subspecific names possess no unique value and are better eliminated from nomenclature. The subjectivity of measurement, however, does not invalidate the subspecies or any other concept. Such yardsticks are used in many disciplines and are considered necessary evils rather than reason for discarding a theory, e.g., prior to use of the thermometer temperature was very subjectively measured and probably resulted in widespread controversy.

Criticisms of the subspecies will probably lead to modification of the original inferences but neither the original infer-

ences nor the opposing views have been established. There must be a great many valid pictures of natural populations already portrayed, but because of the unreliability of general taxonomic practices there is a need for even more meticulous studies. The character of units below the species can be determined and the subspecies segregated from other infraspecific groups only if sampling and analysis of data are raised to the highest accuracy possible.

Any evaluation of subspeciation is no better than the data and analysis providing these conclusions. Evidence against the concept, most of which is based on proposed subspecies, might exist because the original work was not reliable. Reliability of any study is dependent upon the sampling method and the laws of probability, factors frequently ignored in past taxonomic practice. For example, anyone with sufficient training is likely to find variations among collections if he is looking for them. If the possible bias of looking for contrasts is to be avoided, diagnostic characters must be selected *before* seeking specimens for final analysis; hence preliminary study is necessary. Also, discovering a handful of "morphologically and biogeographically unique" specimens does not establish a subspecies new to science. Yet these or similar procedures, ignoring the laws of probability, have often been justified by the excuse of amount of material available to the taxonomist. Data of these kinds have been used both to establish and to reject subspeciation, but they are not reliable for either proposal. Therefore, further deliberation on taxonomic methods should contribute to the question.

The only consideration of this paper is the development of methods with sufficient reliability to accurately analyze the morphological characteristics of subspecies and other infraspecific groups. Developing methods that properly evaluate subspecies in nature involves considering the problems inherent in such investigations and providing means of accurate interpretation of data. Both aspects are concerned in sampling and reliability of data which are treated as separate items in two sections. Sampling is reviewed under the topic of preliminary study and laws of probability under quantitative methods. This is purely a matter of convenience, because both are integral parts of one another. The recommendations are generalized to be applicable to most studies of degree of difference at any taxonomic level. No attempt is made to explore difficulties that are unique to any particular group of organisms, but it is believed most of these difficulties will be made apparent.

Preliminary Studies

Although biologists have a common problem in determining the best way to analyze data, the field biologist has the unique task of obtaining truly representative examples of natural populations. Sampling and other aspects of quantitative systematics are dealt with in some detail by Dice (1952b). Dice indicates that only random sampling can eliminate the biases possible in collecting. The purposes of the present section are to discuss certain sources of collecting bias beyond the scope of Dice's paper and to suggest a form of preliminary study designed to account for these items. This method, involving the sampling of natural populations and statistical analysis of the data, is an attempt to provide a valid final analysis.

Collecting Bias. Aside from the use of the best methods of applying probability statements to taxonomic results, the main difficulty lies in the way the animals are obtained. Unfortunately too many taxa are named on the basis of specimens captured in a haphazard manner. Little if any data other than locality, date and collector is available for these specimens. As with most data acquired in such a manner, trends can be found. These trends

might not be present in nature but be due to unplanned collecting.

Sampling can produce unreliable data for many reasons. Selected ecologically or morphologically "representative series" should be avoided because any choice of material is likely to be subjective. If collecting is essentially restricted to season of ready availability and a seasonal morphological difference exists, a true picture of the species is not obtained. Size comparisons can be in error if the larger individuals are not kept or other selection occurs because of storage or other considerations. Seeming differential morphology also can be caused by long and varied periods between collecting and preserving. Although obvious sexual dimorphism or age changes might be observed and accounted for, slight unrealized deviations can again bias results. Also, specimens from one locality might be grouped together regardless of microhabitat occupied. If subpopulations are fossorial and aquatic and morphological reflection exists, the portion more readily gathered might invalidate data. For these and other reasons, widely practiced collecting procedures can lead to erroneous conclusions.

Haphazard collecting procedures must be avoided especially in the case of seasonal and habitat variations in measurements. The author found that marked morphological changes take place during the annual cycle of the rough-skinned newt, *Taricha torosa granulosa* (Skilton). Unless ratios or other devices can be found to eliminate the effect of such variations there is no accurate means of geographical comparison of seasonally varying structures. Such organisms from two or more localities might show morphological divergences that reflect time of year rather than different taxons. Attempts to cope with these characters in the rough-skinned newt caused the author to believe that they are best eliminated from taxonomic treatment in *Taricha* and that one subspecies is not valid. It seems that similar situations exist in certain other salamanders and in many completely unrelated forms. Habitat variations in morphology might be rare in organisms but an example was found in the plethodontid salamander *Aneides ferreus* (Cope). There are two color phases, each associated with a specific microhabitat, one within rock slides and the other within logs. In certain areas of western Oregon both microhabitats and color phases are found together, but in western Oregon the "log phase" tends to be more prevalent. In many areas of southwestern Oregon and northwestern California rock slides and that color phase are much more pronounced. It is easy to imagine how unrepresentative collections could erroneously indicate two subspecies on the basis of color. Also, separate taxa might be overlooked by ignoring habitat correlations with structure. Such was probably the case in western garter snakes, *Thamnophis* (Fox, 1951).

Museum specimens are a source of error discussed by Dice (1952b). They can not be used because copious microhabitat, etc. data are usually lacking and the above, as well as other, sources of inaccuracy might be present. Even if such data were available and the samples were random samples, lack of uniform preservation might cause a bias due to varying degrees of shrinkage. Bleached color patterns often reflect means and duration of preservation, so color and sometimes pattern must be eliminated as characters. However, the great importance of museum specimens must not be minimized. These specimens can continue to be clues to the need for investigations and sources of conclusions about variability, distribution, etc.

All previous plus other considerations can introduce an unknown amount of bias, because each contributes to non-random samples. They are non-random because every individual of the population does not have the same chance of being collected. Organisms acquired in this

manner result in description of an unknown segment of the entire species. This segment does not give a valid indication of the species, or any definable part of it, unless none of the sources of error are expressed morphologically and haphazard collecting is not significantly different from random sampling. Because the effects of factors are not known until proper collection and analysis are made random samples are essential.

Although few statistical texts treat sampling completely enough to emphasize its importance, Yates (1949) gives a thorough treatment of the subject. His remarks on two aspects of surveys are particularly relevant to present discussion. First, it might seem that very large samples would eliminate many sources of inaccurate conclusions; but they may augment them because as sample size increases the relative error due to random sampling decreases and that to bias increases. This does not make all large samples invalid, but when a possible influence on data dependability is present small samples become mandatory. If one were to minimize bias by treating the factors separately and using random sampling, large samples could be used. Second, even if the above are properly controlled, non-random collecting might result because living organisms do not readily lend themselves to random sampling procedures. Yates (Chap. 2) discusses and gives examples of the bias caused by improper sampling. He (p. 17) also gives a ray of hope to this dismal picture by stating, ". . . in surveys which have as their main objective the comparison of different groups of the population a bias which is approximately constant from group to group will be of little importance. The investigator must also avoid attaching exaggerated importance to minor sources of bias which, in fact, can only produce errors which are trivial relative to the random sampling error." This probably applies to many taxonomic studies or there would be no stable taxa, but errors can be perpetuated when a series of workers all base their conclusions on the same specimens. Also, there are many cases where these biases seem not to have been negligible, e.g., cases where well established diagnostic characters are later found to be of little value.

Present collecting methods will undoubtedly continue and much knowledge will be gained. If biases are not too large the results will be fairly dependable. However, the worker has little chance of knowing what biases exist and how large they are. Therefore, assurance of accuracy will necessitate more definitive procedures, including preliminary studies.

Preliminary Study, Experimental Design. The method of choosing a sample is called the design of the experiment. By implication this includes the analysis of the data, hence the statistical method involved in the study. The most used statistical methods in taxonomy at the present time are adaptations of Student's *t* test. The *t* test should not be used when studying more than two populations, e.g., comparing more than two samples, and one cannot assume he is studying only two biological populations (subspecies, etc.). Numerous other statistical devices are in use. Many of these have merit but most do not satisfy the taxonomist's needs in preliminary investigations.

The best experimental design for preliminary studies leads to a single type of statistical method, the Analysis of Variance. However, the Analysis of Variance is not helpful for final studies of subspeciation because it considers taxonomically insignificant levels of divergence on the order of those population geneticists have shown to exist between many localities. There are many reasons why the Analysis of Variance is "ideal" for preliminary studies. It discovers minute factors that together can alter the taxonomic picture as well as emphasizes individual sources of large error. In addition precision is gained by seeking all possible sources of altering valid conclusions in a single in-

quiry. Also, small samples from several localities are more precise than the same number of specimens from fewer localities. Furthermore, it is suitable for both continuous and discontinuous variates.

There is no perfect experimental design for taxonomy at the present time and perhaps there never will be. Some bias or other error can never be eliminated because of human failings and the characteristics of biological populations; but much is avoided by basing the definition of the species on the portion of the entire species population that can be and is investigated. Doing this may necessitate eliminating certain specimens associated with mentioned conditions but this is the only way that the sampling technique will obtain data on a known population. Future workers, studying a greater portion of the entire species, may extend or restrict the conclusions, but the taxonomist applying the methods to be developed can be assured that his work, based on the populations he sampled, was valid. It cannot be overemphasized that the sampling method should be based on all available knowledge of the animal studied.

Another way of stating the reason for the need of preliminary study is that the results may be invalidated due to statistical interaction. If interaction, caused by sampling "through distinct microhabitat and/or seasonal populations," etc., in different localities, is present, sampling methods might show seeming taxonomic significance among localities. Unless proper design and the Analysis of Variance were used in a preliminary study, i.e., one that would discover interactions, the taxonomist would not be sure what results truly indicate. That microhabitat, seasonal, sexual, age, etc., differences do not have interactions is possible, but one cannot make such an assumption.

One of the best sampling methods might be to consider each collecting area a distinct collection of populations, the individual populations being the various sex-microhabitat, etc., combinations, and to sample localities approximately equally spaced geographically. Defining the microhabitats to be compared is subject to judgment so it should not be treated lightly. The most valid procedure might be to separate as many microhabitats as can be identified. Slight variations among the mean measurements of the animals in each environment might not seriously enlarge the experimental error, but morphological forms, as found in *Aneides ferreus*, would. The larger the geographic area of the individual populations sampled, the greater is the likelihood that two or more genetically different populations will be concluded to be a single population. This often has resulted from having too few specimens from a large area. It is valid to keep the data from all collecting sites separate and to analyze sites individually, but it is incorrect to lump them by any preconceived notions, e.g., biogeographical regions, morphological similarity, etc. Using statistical or any other devices in the latter manner can lead to errors, such as naming three or more subspecies as two, or members of a cline as subspecies. This is further support for Yates' suggestion of using small samples.

Proposed Preliminary Study. Below is a proposed method for preliminary study of an organism. A few localities, at the very least two, but preferably five or more, throughout the range of the organism should be so studied to expose possible sources of bias. If sources of errors are not found, collecting can be simplified. In this instance present methods concentrating on obtaining fifteen or more organisms from single localities might be, but can not be assumed, just as valid as attempts at random sampling. The work of Klauber (1941) indicates present collecting methods to be valid for rattlesnake key characters.

Preliminary study is accomplished as follows:

1. From the known range of the form choose at least two, preferably more, localities to be sampled. This choice will

have to be made according to availability of specimens in different areas, but populations studied should be as equally separated geographically as possible. Fortunately, localities need not be chosen at random.

2. Grid each locality into quadrats. This can be done on a map of the area (Dice, 1952*a*, p. 29). Using a random number table (Dixon and Massey, 1957, sec. 4–3), choose one quadrat at random. Quadrats can be found with sufficient accuracy by pacing. If enough animals are not found in the first quadrat, choose a second and as many others at random as necessary to obtain the desired number of animals. Collect each selected quadrat completely. If N is the number of animals in a sample (N should equal at least fifteen), one must have N males and N females from each microhabitat of each locality. Equal sample sizes are needed because comparisons of individual samples can be made only if equal numbers of individuals are obtained. To accomplish this one may have to take subsamples of samples larger than N by using a random number table. One must keep the males from each microhabitat of each locality separated from the females. If five microhabitats are studied in each of five localities, there will be twenty-five containers with males and twenty-five containers with females. The sexes must be separated, so this may necessitate immediate sacrificing of animals while collecting to enable sexual distinction.

4. Preservation of animals must be rigidly uniform and immediate so little morphological change can take place due to the effects of preservation or captivity.

5. One factor that should be studied is the possible morphological effect due to time of year. The use of the present sampling technique to obtain animals in nature, then measuring and marking, followed by releasing them for future rechecking would be the ideal method for establishing the morphological effect due to season. It would be up to the individual worker if he would be willing to accept laboratory data on seasonal variation.

6. If one's sampling satisfies the above criteria, he can proceed by using the Analysis of Variance to determine whether significant differences exist.

Preliminary analysis will determine the comparisons of the definitive study. Significant differences in sex, microhabitat and season will necessitate two different solutions. Microhabitat and sex are solved in the same manner—consider significantly different microhabitats separately on a geographical basis as is usually done when sexual dimorphism occurs. If seasonal variation occurs attempt to correct for it (ratios, etc.). If correction is not possible eliminate such seasonally variable characters from taxonomic consideration.

Sampling methods for the final analysis will be determined by the preliminary study. Although it would be ideal to have equal sample sizes for definitive diagnosis, it will not be necessary in the method to be presented. The specimens for final analysis must be completely new because use of material from the preliminary study will bias the results.

Notes on the Statistical Analysis. Most individuals involved in taxonomic work have access to the services of a statistician. For this reason, the complex calculation procedures are not considered. It is sufficient for the systematist to know that, if seasonal variation is studied separately, he is working with a three variables (locality, sex and microhabitat) of classification Factorial Design, a type of Analysis of Variance, with equal numbers of observations per subclass. A fourth variable of classification might be used to compare conventional sampling methods with attempts at random sampling.

Those workers who use the Analysis of Variance might not be familiar with certain tests that can be used to justify the assumptions (Dixon and Massey, 1957, pp. 179–181, 226–227). If the assumptions

are not justified, transformation of data will make them valid (Li, 1957, Chap. 23). Because many biologists are reluctant to use transformations, attention is called to Li's remarks in the introduction to the chapter cited. If significant differences are found in the Analysis of Variance, many methods are available to find where the differences occur (Li, 1957, Chap. 15).

One of the most valuable types of statistical method is that which determines sample size (Cochran and Cox, 1957, sec. 2.2). This procedure enables reliable predetermination of the minimum difference between population means that will be disclosed in future investigations. Taking this step gives a valid basis for sample size. It might justify the use of fewer than 15 specimens per sample.

Although the proposed methods are time consuming, and perhaps impossible in many studies, an investigation using these procedures would often take little longer than techniques used in most critical studies. With the preliminary study even greater precision is obtained with fewer specimens and localities and a shorter time in the field. Studies of this type should provide a fertile field for workers without time and funds for more extensive research problems.

Quantitative Methods in Taxonomy

There are three primary approaches to the separation of subspecies. First is the technique of observation and separation by a well-developed "biological sense." There are too many examples of accurate application of these intangible devices in the study of species to deny their validity. However, they do not supply the quantitative statements of character variation necessary for critical descriptions and diagnoses of subspecies. Second are many statistical methods, ranging from the simple *t* test to multivariate analysis. In any of these, significant differences between or among samples are assumed sufficient for separation. These methods should not be considered because they can "split" almost identical populations, e.g., very large samples can discern separation between populations having 95%, or more, overlap in diagnostic characters. Finally are the techniques of emphasizing degree of diversity used by most critical workers. Two approaches are involved; one is statistical, and the other, simplification and approximation of statistical methods. The latter are less desirable because they are not reliable and cannot be made so. The former, which include graphic analysis, are of sound statistical basis, therefore superior. Because statistical methods may seem complex and be imperfectly understood, there may be a tendency to accept one of the simpler approaches. However, it does not seem reasonable that the taxonomist who has spent countless hours in the field and laboratory would be willing to sacrifice precision of analysis, hence accuracy of conclusions, to save a few hours of time.

In addition to the above methods there is an ingenious device proposed by Womble (1951) for the simultaneous consideration of many characters. Unfortunately it lacks reliability because taxonomic data are subject to sampling errors. However, it is strongly recommended that Womble's paper be consulted when interpreting the results from the many measurements which must be studied.

Of all the above methods graphic analysis is preferred. Graphic analysis is a brief, comprehensive and simple summary of statistical methods used to estimate the divergence among populations. This divergence is measured by character average and variation, which are represented mathematically by the mean and standard deviation. The resulting graphic portrayal of morphological differentiation with other biological data gives the taxonomist a sound basis for concluding that samples represent one or more subspecies. However, the graph needs reconsideration because it lacks reliability. Without reliability interpretations are applicable to the samples and not necessarily to the com-

plete populations. Therefore, the primary purpose of this section is to modify the existing graphic analysis so probability statements can be made about the total populations in nature. A second graph is developed for characters that are either present or absent in an organism.

There is no inconsistency in the fact that a calculation from a sample, called a statistic, can be valid but not reliable. Statistics must be linked with other computations to provide proper prediction of true population values. Reliable estimates of true values take the form of ranges, called confidence intervals. The method of obtaining confidence intervals has a known reliability, i.e., probability of producing ranges including the estimated value. Statistics without confidence intervals have unknown reliability in predicting population values. For example, the sample mean, or average, is the most efficient estimate of the true average, the population mean, but the accuracy of the sample mean in estimating the population mean is not known. To obtain a reliable estimate of the population mean, a confidence interval must be calculated.

There have been four primary contributions to graphic analysis. Ruthven (1908) graphed the range and mean and included the size of the sample. Dice and Leraas (1936) attempted to differentiate among samples by adding a rectangular bar outlining two estimated standard errors of the sample means on each side of the sample mean. When the Dice-Leraas paper was published there was no adequate way of comparing many samples of the type generally encountered by the field biologist. Also, the consequences of comparing many sample means and estimated standard errors were not fully realized. Because the method gave reasonable results, it received wide adoption and has been improved upon. Hubbs and Perlmutter (1942) added the sample standard deviation to the graph in an attempt to separate 84 percent of one population from 84 percent of another. These refinements, like those of Dice and Leraas, made sense in practical problems and have also come into general use. Hubbs and Hubbs (1953) refined graphic presentation (Fig. 1A) without any new mathematical considerations. All these methods gave acceptable results because they are basically sound.

Although the graphic method has gained wide acceptance, the amount of divergence necessary for subspecific recognition is a topic of controversy. This subject is reviewed by Mayr, Linsley, and Usinger (1953). The author is not recommending any particular degree of separation between populations before subspecies are to be designated. Only field studies can establish a definite subspecific "rule" indicating the minimum degree of separation. In the present paper the recommendations of Hubbs and Perlmutter (1942) have been followed, i.e., non-overlap of 84 percent of each population, but consideration is made of other degrees of separation in the hope that one of these will later be proven proper.

This section develops two methods of graphic analysis that are subject to probability statements, which in turn are dependent upon random sampling. Neither of these methods are ideal. A research statistician with knowledge of the problems of systematic studies might be able to offer greater refinement. However, of the methods available the combinations considered are the most valid and reliable. One graph is for continuous variates, i.e., numerical values that can approximate any value on a continuous scale. The graph is merely a modification of the graphic method as presented by Hubbs and Hubbs (1953). The other graph is for discontinuous variates that fall into only two classes, e.g., presence or absence. Discontinuous variates are numerical values that can occur only as whole numbers. Data of this kind are often considered more meaningful than they really are, e.g., a series of five entirely different colored forms of a species do not display sufficient reliability to be named a new

subspecies. This graph is a simple application of a statistical method to taxonomic data. Development of both graphs necessitates consideration of certain aspects of statistical theory leading to a measurement of statistical probability, the confidence interval. Confidence intervals will be developed for the population mean and standard deviation. These confidence intervals will be the only modification of the present method of graphic analysis of continuous variates.

Population vs. Sample; Confidence Intervals. Modifications of the present methods of graphic analysis are essential because they do not distinguish between population and sample. A sample in taxonomy is merely a segment of all individuals of a species, subspecies, restricted locality, etc., which constitute the population. Distinction between population and sample in any scientific study is mandatory. Although mathematical proof of this need is readily found, such proof leaves much to be desired by many using statistical methods. A solution to this difficulty is found in texts that combine sampling experiments with simple algebraic proof of statistical methods. Both Li (1957) and Dixon and Massey (1957) are excellent texts that utilize this type of proof. The need for distinction between population and sample means, and measurements of reliability for sample means can be appreciated by considering chapter five of Li's book.

Lack of distinction between population and sample by some biologists may be the result of using statistical symbols identical or similar to parameter symbols of the statistician. Most statisticians use the following notations: μ (population mean), $\bar{x}$ (sample mean), σ^2 (population variance), s^2 (sample variance), σ (population standard deviation), s (sample standard deviation), $\sigma_{\bar{x}}$ (standard error of the population mean, or standard deviation of the sample means), $s_{\bar{x}}$ (estimated standard error of the population mean, or estimated standard deviation of the sample means), etc. Notations in general use by biologists are M (sample mean), σ^2 (sample variance), σ (sample standard deviation), σ_M (estimated standard error of the population mean), etc. One cannot ignore the fact that statistics are only approximations of parameters and additional measures must be taken to obtain reliable estimates of parameters.

Obtaining reliable estimates of parameters from statistics is accomplished by a branch of statistical methods called estimation. Estimation is a method of using statistics to form a range that will include a population parameter with a certain degree of reliability. This calculated range is called a confidence interval; the limits of the range, confidence limits. The degree of reliability of such a range is represented by a confidence coefficient. In using such confidence intervals, or limits, for all possible samples of a given size from a population, a chosen percentage, indicated by the confidence coefficient, of such intervals will include the population parameter. It is surprising that Mayr, Linsley, and Usinger (1953) consider that these intervals are difficult to calculate. Confidence limits for population means add nothing to present graphic method calculations; those for population variances add a simple division. It is recommended by statisticians that the 95 percent or 99 percent confidence intervals be used; 95 percent or 99 percent would be the confidence coefficient. The 95 percent confidence interval of the population mean is $\bar{x}+t_{.975}s_{\bar{x}}>\mu>\bar{x}+t_{.025}s_{\bar{x}}$, where the t values are percentiles of the t distribution. The 95 percent confidence interval of the population variance is $s^2/P_{.025}>\sigma^2>s^2/P_{.975}$, where $P_{.025}$ and $P_{.975}$ are the 2.5 and 97.5 percentiles of the Chi-squared over the degrees of freedom distribution, symbolically χ^2/d.f.

Confidence limits are based on the sampling distribution of the statistic estimating the population parameter. This is the distribution formed from the values of a

statistic calculated from each of all possible samples of the same size from a population. The distribution of sample means from a normal population follows the normal distribution. As the size of the sample increases, the distribution of the sample means of all possible samples of the same size from any population, regardless of its distribution, becomes more and more like a normal distribution provided that the population has a finite variance. The criterion of a finite variance is met in taxonomic studies. Any normal distribution is delimited by two parameters, μ and σ. The population mean locates the curve and the population standard deviation determines the spread of the curve. Because the sample means follow the normal distribution, or approximate it, the mean and standard deviation of all sample means will delimit the distribution. The mean of all sample means is equal to the population mean ($\mu_{\bar{x}}=\mu$). The variance of these sample means is equal to the population variance divided by the size of the sample ($\sigma^2_{\bar{x}}=\sigma^2/N$) and the standard deviation of the sample means, called the standard error of the sample means, to the square root of this quantity ($\sigma_{\bar{x}}=\sigma/\sqrt{N}$). In estimating μ from $\bar{x}$ and $\sigma_{\bar{x}}$ the 95 percent confidence interval ($\bar{x}+1.96\sigma_{\bar{x}}>\mu>\bar{x}-1.96\sigma_{\bar{x}}$) will include the area of the normal curve in which one expects to find 95 percent of all possible sample means of a given sample size. The factor 1.96 is used because between plus and minus 1.96 standard deviations of the normal curve are found 95 percent of the observations, and the sample means follow or approximate the normal distribution. The value 1.96 is used when $\sigma_{\bar{x}}$ is known. Because only the estimated standard error ($s_{\bar{x}}$) is known from a sample one cannot use 1.96. The fact that the true value of the standard error is unknown should be sufficient to appreciate this. Because the confidence limits will be formed with an estimate of $\sigma_{\bar{x}}$ the reliability of that estimate must be considered. To obtain this reliability and maintain the level of the confidence coefficient, one must refer to a table of the *t*-distribution and estimate 95% confidence limits of the population by the formula $\bar{x}+t_{.975}s_{\bar{x}}>\mu>\bar{x}+t_{.025}s_{\bar{x}}$. The confidence interval of the population standard deviation is obtained from the confidence interval of the population variance. Simpson and Roe (1939) contains an inaccurate belief of the time that the distribution of sample variances from a population with a normal distribution is in turn normally distributed. Unfortunately this error is continued by direct statement or implication in the primary reference works in quantitative systematics (Cazier and Bacon, 1949; Mayr, Linsley, and Usinger, 1953). Because the distribution of s^2/σ^2 follows the Chi-squared over the degrees of freedom distribution and not the normal distribution, the percentiles are taken from that table to determine σ^2 by confidence limits ($s^2/P_{.025}>\sigma^2>s^2/P_{.975}$). The confidence interval of the population standard deviation is the square root of the confidence interval of the population variance. The confidence interval of σ will contain a value greater than s and a value smaller than s. The larger value must be used in the graph to insure reliability of our estimates. In effect only half of the confidence interval is used, so one obtains the 95 percent interval by using the 90 percent coefficient, $P_{.05}$ and $P_{.95}$. No such problem exists in the confidence interval of the population mean because the entire estimate is utilized.

It is to the advantage of the taxonomist to reduce the range of confidence intervals so more critical diagnosis of true difference is possible. Confidence intervals are reduced by increasing the sample size. Increasing the sample size decreases the values of *t* and χ^2/d.f., as well as $s_{\bar{x}}$. This indicates that the magnitude of confidence intervals is directly related to sample sizes, the larger the sample, the smaller the confidence interval.

Graphic analysis has invalid tests of significance that are related to confidence in-

tervals. Significant differences among sample means are indicated by degree of overlap of the sample means plus or minus twice their estimated standard errors ($\bar{X} \pm 2s_{\bar{X}}$). Comparison with the above confidence limits of the population shows that this test of significance of the differences among sample means is identical to confidence limits for the population mean except for the factor 2 instead of t. The factor 2 would be for the 95.45 percent confidence limit of an infinitely large sample, i.e., $\sigma_{\bar{X}}$ is known. The tests of significance are not invalid because they are similar to confidence intervals. They are invalid because the estimated standard error of the sample means cannot be used to determine the significance of the differences among sample means. The invalidity results from the close mathematical relationship between the mean and standard error comparison and the t test. The t test is limited to determining the significance of the difference between two sample means. Extension of the t test to compare three or more sample means is invalid because more than two comparisons increases the probability of t tables indicating a significant difference when none exists. Testing the significance of the difference among more than two samples is accomplished by the Analysis of Variance, but if standard errors are used to compare five and ten sample means, one must use three and five estimated standard errors of the sample means respectively as a crude approximation to a valid test. It follows that the graph does not provide a valid method for testing the significance of the differences among a number of sample means.

The proposed changes are not conservative measures. Actually one might consider these changes not conservative enough in estimating population means. This is true because the confidence limits are formed for the purpose of comparing sample differences. Therefore, these multiple comparisons are subject to the same source of error as comparing many sample means and twice their standard errors for tests of significance. It is believed, however, that if this limitation is kept in mind the present changes will provide a sufficient degree of reliability in distinguishing among subspecies.

Comparing Many Samples. Graphic analysis has been used for two primary purposes, determining significant differences among sample means and indicating subspecific differentiation. The value of a graph that determines significant differences among sample means is debatable. Population geneticists have shown on theoretical grounds, and in field studies, that significant differences should exist among different populations of a species. Modern taxonomists have accepted the existence of such differences and the premise that most of these differences are not of taxonomic significance. On the other hand, an indication of subspecific differences is of value and will remain the primary purpose of the modified graph. However, the proposed modifications do more than indicate degree of morphological differences suitable for subspecific recognition. Possibilities of future studies are suggested because larger samples might decrease the magnitude of the confidence intervals of population mean and standard deviation.

In any method used to indicate degree of difference between populations the population mean and standard deviation must be estimated with a high degree of accuracy. For this reason the modified graph (Fig. 1B) contains confidence intervals for both parameters. The graph also symbolizes the sample range of variation as did previous graphs. The 95 percent confidence interval of the population mean is indicated by the central blackened bar of length $t_{.025}s_{\bar{X}}$ to $t_{.975}s_{\bar{X}}$ centered on the sample mean (indicated by the small narrow triangle projecting above the center of the blackened bar). The confidence interval of μ is similar to the central quantity of the previous graph (Fig. 1A) but the estimate of μ is not included with the intention of being used for tests of significance of the differences among

sample means. The 95 percent confidence interval of the population standard deviation is indicated by the entire open rectangle. At the outer extreme of each open rectangle is enclosed another rectangle with included vertical and horizontal lines. From the vertical line inward to the blackened bar is represented the magnitude of the pooled sample standard deviation. The horizontal line represents the magnitude of the 90 percent confidence interval of the population standard deviation. Because only the non-overlap of outer extremes of open rectangles indicate subspecific differentiation, i.e., only the greater value of the confidence interval of σ is considered, the 90 percent confidence interval is in effect a 95 percent confidence interval. In previous methods the magnitude of the sample standard deviation was indicated by one-half of each black bar plus the adjoining white bar. This greatly underestimated reliable endpoints of possible population variation. The correctness of the previous method is dependent on two improbable events, that the sample mean equals the population mean and that the sample standard deviation equals the population standard deviation. The horizontal solid line indicates the sample range. The sample size in practical problems would be indicated by a number in brackets after each locality name.

Although the modified graph is devised to show 84 percent non-overlap between populations, other levels of differentiation are easily applied. Higher degrees of separation are obtained by adding a multiplier to the confidence limit of the population variance. The multipliers and levels of separation are as follows: 1.25 for 90 percent from 90 percent, 1.50 for 93 percent from 93 percent, 1.88 for 97 percent from 97 percent, 3.00 for 99.7 percent from 99.7 percent and 3.24 for 99.9 percent from 99.9 percent.

An additional step should be taken to increase the ability of the proposed graphic method to discover reliable differences. Tests for homogeneity of variances are likely to indicate that the sample variances are all estimating a common population variance. This allows pooling of all sample variances into a single estimate of the population variance. The confidence interval of σ will be of narrower range than individual sample confidence intervals because the estimate of a common population variance is based on many more observations. Due to this innovation all open bars of the graph will be of identical size. Even if a test for homogeneity of variances indicates that all sample variances are not estimating the same population variance, the data can be transformed to a scale where this is true. The pooled sample variance also provides a more reliable value to calculate the various estimated standard errors of sample means so it should be used instead of the individual estimates from each sample.

These proposed changes in previous graphs have two distinct advantages. First, by using a test for homogeneity of variances and obtaining a pooled sample variance, an estimate of σ is provided regardless of the sample sizes. Previous modifications of the method did not include this estimate for small samples. Second, probability statements can be made about the various parameters. In the author's opinion there is an additional advantage in that the method will cause slight increase in the ranges of parameter estimates based on large samples but will show marked increase in estimates based on small samples. Therefore, subspecies will have to be based on more than a type and a few paratypes.

The process of calculating the confidence limits for the graph can be reduced to a few steps. Unless otherwise indicated the citations to methods are to Dixon and Massey (1957). The calculation procedure is as follows:

1. Calculate the sample mean (sec. 3-1) and sample variance (sec. 3-2) for each sample. Note that the sample variance

must be divided by N–1 rather than N (sec. 4–5).

2. Use Cochran's test (pp. 180–181) for testing the homogeneity of variances. If the test is significant proceed to step 3. If the test is not significant proceed to step 4.

3. Choose the appropriate transformation so Cochran's test is not significant (Li, 1957, Chap. 23).

4. Pool all sample variances into a single sample variance (sec. 8–5).

5. Calculate the confidence limits of the population means (sec. 6–6).

6. Calculate the confidence limits of the common population variance using the pooled sample variance (sec. 6–7). Take the square root of this quantity to obtain the confidence limit of the population standard deviation.

7. Graph the confidence intervals.

Table I contains the raw data and calculations necessary for the previous graph (Fig. 1A) and present graph (Fig. 1B). The only additional calculations needed for Figure 1B are the confidence interval calculations for the five population means and population variance common to the five populations. The data for the table were obtained from the Dixon and Massey table of random normal numbers (p. 371). The five samples were the first five, ten, fifteen, twenty, and twenty-five random normal numbers from columns one to five respectively. A trend was created in the data by adding 10.0, 10.4, 10.8, 11.2, and 11.6 to progressive samples which caused those values to be known population means. The population standard deviation for all samples remains one, i.e. $\sigma=1$.

Comparing the previous graph with proposed modifications one finds that the first sample mean plus twice the estimated standard error of the sample means does not include the true value of the population mean. Also, because of chance twice the estimated standard error of the sample means is less than the standard deviation. This estimate of the population standard deviation is extremely low. Notice also that only one sample standard deviation is closer to the true population value of one than is the pooled sample standard deviation.

Although this graph is considered only for continuous variates, certain discontinuous variates can be applied to it. However, most discontinuous variates must be transformed in some manner before normal distribution statistics can be applied. The chapter on transformations already cited from Li considers the necessary transformations.

Dichotomous Characters. Graphic representation of characters that fall into two classes, presence or absence, is possible. This is enabled by the availability of tables and calculation approximations of these tables (Snedecor, 1946, sec. 1.3; Li, 1957, sec. 21.5). The graphic method is based on the confidence interval of the mean of a binomial population. Any statistical textbook that considers the binomial distribution shows that the population mean is the relative frequency, which can be considered percentage occurrence, of a character. For this reason two 95 percent confidence intervals of two population means showing the required non-overlap would indicate subspecies, e.g., 84 percent from 84 percent, would be exactly indicated by the two confidence intervals, 0–16 percent and 84–100 percent. This requires moderate sized samples. The two 95 percent confidence intervals would be based on two samples of 22 specimens each, one sample not showing the character (0–16 percent 95 percent confidence interval) and the other having all specimens showing the character (84–100 percent 95 percent confidence interval).

The graph for discontinuous character (Fig. 2) is very different in appearance from that for continuous characters. From approximation calculations or tables the 95 percent confidence intervals are obtained and graphed as horizontal lines. Each horizontal line on the graph represents an individual confidence interval.

TABLE I—DATA AND CALCULATIONS FOR CONTINUOUS VARIATE GRAPH

σ	1.0	1.0	1.0	1.0	1.0	
μ	10.0	10.4	10.8	11.2	11.6	
	10.46	10.53	10.48	10.88	11.54	
	10.06	7.88	10.61	11.01	12.14	
	11.48	9.05	11.49	11.89	12.52	
	11.02	9.93	14.32	14.72	12.17	
	11.39	9.85	11.12	11.52	15.54	
		9.89	11.39	11.79	12.48	
		8.35	10.80	11.96	12.57	
		9.92	10.64	11.07	13.63	
		11.76	9.19	10.86	11.09	
		10.63	11.17	11.96	11.78	
			10.75	9.98	11.12	
			12.15	10.64	11.35	
			9.69	12.79	11.65	
			10.81	10.48	12.74	
			9.89	12.43	11.41	
				12.24	11.10	
				11.56	10.61	
				11.62	12.57	
				12.57	12.59	
				10.33	10.51	
					11.85	
					12.86	
					10.68	
					11.38	
					11.03	
sum	54.41	97.79	164.50	232.30	298.91	
N	5	10	15	20	25	
$\bar{x}$	10.88	9.78	10.97	11.62	11.96	
Σx^2	593.5781	967.7407	1823.6954	2719.8460	3602.6709	
$\Sigma(x)^2/N$	592.0896	956.2884	1804.0167	2698.1645	3573.8875	POOLED
SS	1.4885	11.4513	19.5787	21.6815	28.7834	82.9834
s^2	.37	1.27	1.40	1.14	1.20	1.19
S^2/N	.07	.13	.09	.06	.05	
$\sqrt{S^2/N}$	.265	.356	.305	.239	.219	
$2\sqrt{S^2/N}$	.53	.71	.61	.48	.44	
s	.61	1.13	1.18	1.07	1.10	1.09
t	2.776	2.262	2.145	2.093	2.064	
$t\sqrt{s^2_p/N}$	1.35	.78	.60	.51	.45	

95 percent confidence interval of σ $\sqrt{\frac{1.19}{.739}} > \sigma > \sqrt{\frac{1.19}{1.29}}$

$1.27 > \sigma > 0.96$

The vertical line passing through each horizontal line represents the percent occurrence of the particular character. The two heavier vertical lines passing through the entire graph portray the 16 percent and 84 percent presence of a character, the hypothetical limits for subspecific differentiation.

If two samples are to reliably express 84 percent differentiation from one another the confidence interval of one must be completely to the left of the 16 percent line and the other completely to the right of the 84 percent line. In figure 2, 28 samples, 14 showing 100 percent absence and 14 showing 100 percent presence, are

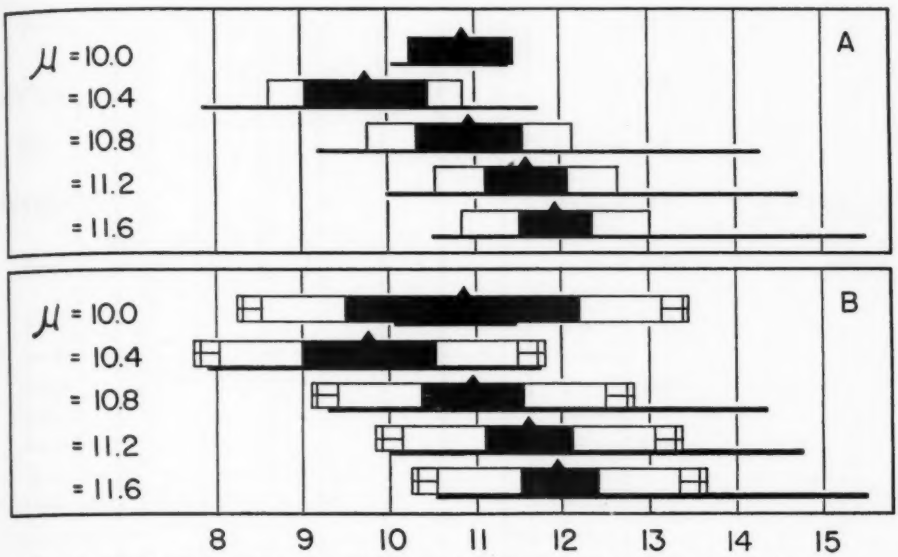

FIG. 1. Graphs for continuous variates and transformed discontinuous variates.

A. Previous graph. The range of variation is shown by a heavy horizontal line; the sample mean ($\bar{x}$), by a small, narrow triangle. The blackened part of each bar comprises 2 estimated standard errors of the sample means ($2s_{\bar{x}}$) on either side of $\bar{x}$. One-half of each black bar plus the white bar at either end outline 1 sample standard deviation (s) on either side of $\bar{x}$.

B. Proposed graph. The range of variation is shown by a heavy horizontal line; the sample mean ($\bar{x}$), by a small, narrow triangle. The blackened part of each bar comprises the 95% confidence interval of the population mean ($\pm t\, s_{\bar{x}}$) and is centered on $\bar{x}$. The open bar represents the pooled sample variance and the 95% confidence interval of the population variance. At the outer extreme of each open bar is included another rectangle with included vertical and horizontal lines. From the vertical line inward to the blackened bar is represented the pooled sample standard deviation (s_p). The horizontal line represents the 95% confidence interval of the population variance.

given for fourteen different sample sizes. This serves to show the increase in reliability that results from larger samples.

For practical problems the graph would have to be modified. Instead of sample sizes localities would be substituted. After each locality the sample size should be included in parentheses, e.g., San Luis Obispo (24).

Figure 3 has been added to show the minimum allowable percent presence for given sample sizes. The curve gives presence values necessary for a minimum of 84 percent of the population to be assumed (95 percent confidence coefficient) to possess the character. This graph can just as easily be used in considering samples whose 95 percent confidence interval will indicate no more than 16 percent occurrence. In this instance 100 percent to 80 percent would be considered 0 percent to 20 percent.

Final Considerations

Many characters must be used to establish the validity of a subspecies. If subspecies are valid, most characters must indicate identical geographic conformations. Naturally, this does not mean that all character divergence must intergrade at every zone of subspecies contact. Cer-

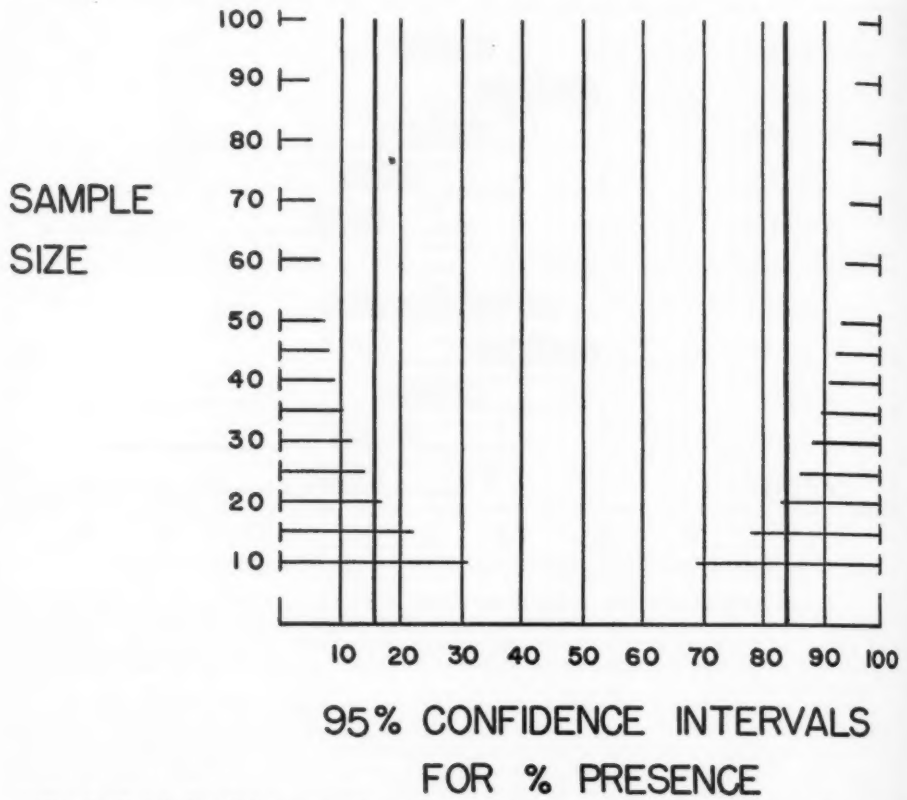

FIG. 2. Graph for dichotomous characters. Horizontal lines each represent a 95 percent confidence interval for percent presence.

tain subspecies can have essentially the same fluctuation in one or more characters, but there must be conformity in the site of differentiation between two subspecies. Absolute conformity is not likely to be indicated by any method of analysis because measurements are subject to random sampling errors and some differential gene flow is possible. Only characters that show a high degree of correlation would tend to have identical breaks. However, only moderate non-conformity to pattern can be allowed as a basis for reliable distinction among geographic races. For these reasons, many, perhaps twelve or more, characters should be used for critical assessment of the existence of subspecies.

Womble's (1951) approach to the study of many characters provides insight into the problem. If very large random samples are considered properly, this method should provide critical analysis. However, samples of such size are not likely to be obtainable. Smaller samples would require confidence limits of the population means to be reliable. Attempts to use such intervals would make this already involved procedure too complex to consider. However, a modification of Womble's graph, summing number of subspecific level differentiating characters, should aid

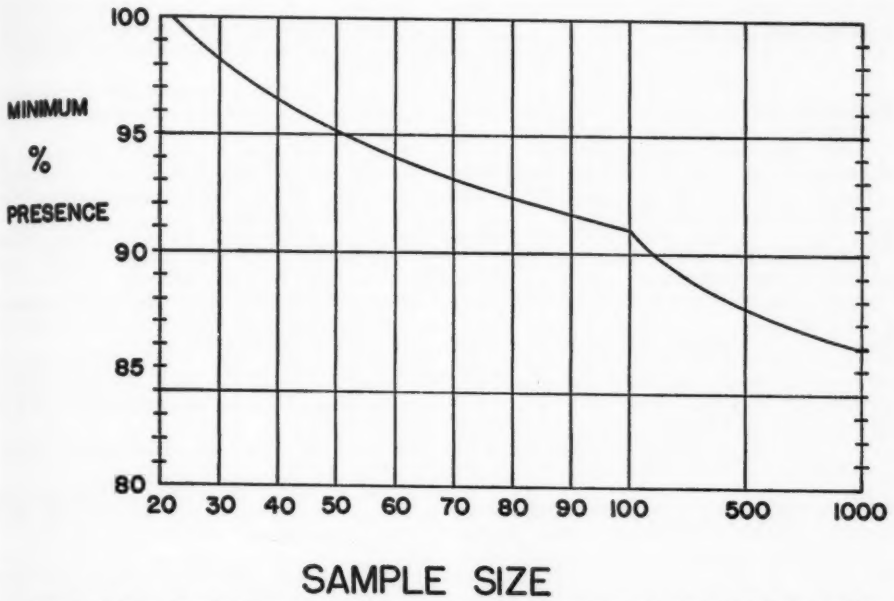

FIG. 3. Curve of minimum percent presence for different sample sizes indicating at least 84 percent of the population can be assumed (95 percent confidence coefficient) to possess the character.

in interpreting the results of most studies. Such a graph would emphasize areas of subspecific intergradation if such exist.

In addition to many characters, many localities must be sampled and considered separately. Each locality must be sufficiently sampled to provide data for a separate consideration. The not uncommon practice of lumping data from different areas is very likely to produce biased results. It is not at all surprising that such data can cause morphological patterns that belie the subspecies concept. Subspecies proponents have forced such patterns to mesh into subspecies. Antagonists have used such methods to weaken the concept. Neither group has "proven" their contentions.

The proposed changes make it more difficult than most procedures to discover subspecies. However, in light of present criticism of the concept, they provide a seemingly necessary addition to investigations. The recommended methods do not consider if populations could be separated into subspecies but if the probabilities are such that subspecies very likely exist.

Summary

Subspeciation seems to be a logical result of neo-Darwinian theory of speciation. Criticism of subspecies may have resulted from the unreliability of general taxonomic methods rather than error in extensions of original theory. Only reliable procedures can provide a true characterization of the subspecies and other infraspecific groups in nature. The primary sources of error in taxonomic methods are in sampling and analyzing data. These possible errors are considered in some detail and improvements in sampling and analysis are proposed. Graphic representation of statistical considerations of data is used because it presents data in a concise manner and facilitates interpretation by other workers. Graphs are developed

for both continuous and dichotomous discontinuous variates.

LITERATURE CITED

CAZIER, M. A., and BACON, A. L. 1949. Introduction to quantitative systematics. *Bull. Amer. Mus. Nat. Hist., 93*:343–388.

COCHRAN, W. G., and COX, G. M. 1957. 2 ed. Experimental designs. John Wiley and Sons, Inc., New York, 611 pp.

DICE, L. R. 1952*a*. Natural communities. Univ. Mich. Press, Ann Arbor, 574 pp.

——— 1952*b*. Quantitative and experimental methods in systematic zoology. *Syst. Zool., 1*:97–104.

DICE, L. R., and LERAAS, H. J. 1936. A graphic method for comparing several sets of measurements. *Contr. Lab. Vert. Genetics, Univ. Mich.*, No. 3, 3 pp.

DIXON, W. J., and MASSEY, F. J., JR. 1957. Introduction to statistical analysis. McGraw-Hill Book Co., New York and London, 488 pp.

FOX, W. 1951. Relationships among the garter snakes of the *Thamnophis elegans* Rassenkreis. *Univ. Calif. Publ. Zool., 50*:485–530.

HUBBS, C. L., and HUBBS, C. 1953. An improved graphical analysis and comparison of series of samples. *Syst. Zool., 2*:49–57.

HUBBS, C. L., and PERLMUTTER, A. 1942. Biometric comparisons of several samples, with particular reference to racial investigations. *Amer. Naturalist, 76*:582–592.

KLAUBER, L. M. 1941. Four papers on the applications of statistical methods to herpetological problems. *Bull. Zool. Soc. San Diego, 17*:1–95.

LI, J. C. R. 1957. Introduction to statistical inference. Edwards Bros., Ann Arbor, 321 pp.

MAYR, E., LINSLEY, E. G., and USINGER, R. L. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., New York and London, 328 pp.

RUTHVEN, A. G. 1908. Variations and genetic relationships of the garter-snakes. *Bull. U. S. Natl. Mus. 61*, 201 pp.

SIMPSON, G. G., and ROWE, A. 1939. Quantitative zoology. McGraw-Hill Book Co., New York and London, 414 pp.

SNEDECOR, G. W. 1946. Statistical methods applied to experiments in agriculture and biology. 4 ed. Iowa State Coll. Press, Ames, 186 pp.

WOMBLE, W. H. 1951. Differential systematics. *Science, 114*:315–322.

YATES, F. 1949. Sampling methods for censuses and surveys. Hafner Publ. Co., New York, 318 pp.

RICHARD A. PIMENTEL is Associate Professor of Zoology at California State Polytechnic College, San Luis Obispo. The author wishes to thank his colleagues for many helpful discussions, criticisms and encouragement. He is especially grateful to Dr. Philip C. Dumas and Dr. William J. Riemer.

General Adaptation and Evolution

WILLIAM L. BROWN, JR.

WITHIN single species of animals (and plants) many characters under genetic control are known to vary in correlation with geographically varying features of the environment. On a local scale, larks (Niethammer, 1940) or mammals on lava flows (Benson, 1933) may vary in color according to the color of the soil on which they live. In such cases, adjacent populations on contrasting soil types may show relatively sharp differences in color. This variation appears to be adaptive in that it presumably renders the animals less conspicuous to predators.

Over broader areas, species show heritable variation corresponding to climate, soil, vegetation, the presence of competitors and predators, and so on. In *Rana pipiens* Schreber, the North American leopard frog, developmental rates, and perhaps also the proportions of the eggs and arrangement of the egg masses, are correlated with temperatures found during the season of reproduction and growth (Moore, 1949). The so-called "Ecological Rules" of Bergmann, Allen, Gloger and others (brief summary by Mayr, 1942) cover many cases of broad-scale variation, most of them probably directly adaptive, though needing closer study. Where variation is more or less continuously graded to form a cline, the term *ecocline* has been used (Huxley, 1943; Auffenberg, 1955) to characterize variations that appear to be adaptively correlated with the environment.

Geographical variation can be strongly influenced by the kinds of competitors present in parts of a species' range. The honeycreeper *Loxops virens* (Gmelin) ranges through most of the main Hawaiian Islands, and shows some variation from island to island, but its most divergent population occurs on Kauai, the only island where a second closely related species of *Loxops* is also found (Amadon, 1950). This phenomenon, called *character displacement*, has been summarized and exemplified in a separate paper (Brown and Wilson, 1956). It seems obvious that prey species should vary according to the kind and density of predators attacking them, to the kinds of distasteful models available for them to mimic, and to the kind and density of other species that are potential prey for the same predators (L. Brower, 1958).

The examples and even the categories of variation correlated with definite, limited aspects of the physical and biotic environment could be expanded virtually without end. It will be appreciated, I think, that the demonstration of these correlations is often no easy matter. Frequently, the apparent environmental correlate of a varying character will really bear only a second-or- third-order relationship to that character, so that puzzling exceptions to the correlation occur.[1]

Where characteristics of a species vary in correlation with definite attributes of

[1] Refinement of study usually resolves such difficulties. For instance, there has been some confusion about Bergmann's Rule, which claims for warm-blooded vertebrates an increase in body size in the colder parts of the range of a species. Now it is beginning to appear that there is a positive correlation between body size and increased aridity that may exceed in significance the size-temperature correlation (Hamilton, 1959). Then, there is Gloger's Rule, which states that melanic pigments tend to increase in the warmer and more humid parts of the range. But for many insects, at least, melanism often seems better correlated with a need during critical seasons for absorption of radiant heat. Thus, insects from continually cloudy or heavily shaded environments that are merely cool or temperate may be darker in color than those from colder areas more open and better insolated during the growing season.

the environment, adaptive relationships are assumed and often proved. Where the adaptive relationship is known or reasonably assumed to hold with a special aspect of the environment, it seems convenient to classify it as a *special adaptation.* Most of the adaptations so far studied as geographical variation are of the special type.

Even considering the frequent subtlety of adaptive relationships, and difficulties attending their investigation, it does seem that we cannot hope to fit all geographical variation into the category of special adaptations. With the recent increase in emphasis on analysis of single-character variation, a growing number of cases is being exposed in which geographical variation is apparently uncorrelated with known environmental influences that might conceivably affect it. On the contrary, such variation often assumes definite patterns (e.g., central-peripheral ones) that seem utterly to ignore the stronger climatic and biotic gradients that cut across them. When this variation is clinal in nature, writers such as Huxley (1943) and Auffenberg (1955) have spoken of *geoclines* or *distance clines,* thought to be due to the isolation imposed by distance alone.

It seems to me, however, that distance pure and simple can be thought of as isolating only in a non-existent static system or for completely neutral genes. If a genetic change arises at a given point in a continuous population or series of contiguous populations not separated by barriers to gene flow, and if the change is adaptively positive, it should spread throughout the system in time. In other words, distance clines are simply spreading adaptations frozen in a single time transect. The concept of "isolation by distance" gives us little real help in understanding geographical variation of the non-correlated type.

Let us look at a few possible examples of patterned variation of the non-correlated kind drawn from the literature. For further examples, those interested can refer to my paper on centrifugal speciation (Brown, 1957).

Figure 1 is the familiar map from Moore's classic (1944) paper on the geographic variation of *Rana pipiens,* showing the distribution of populations sampled in which the males have rudimentary oviducts (solid circles), and of those in which the males lack rudimentary oviducts (open circles). Notice that males with oviducts are found only in peripheral areas, no matter how isolated these are, and regardless of their extremes in climatic, soil, and vegetational differences. Males without oviducts occur in the central populations, roughly corresponding to the eastern temperate forest areas, and they also reach out into a few of the peripheral areas, where they are intermingled with populations of which the males *have* oviducts. I interpret this as the centrifugal expansion of a trait—lack of oviducts in the male—that is "advanced" for this species. We do not know what the adaptive significance of oviductlessness in the male may be; it has not been studied. It could represent sheer metabolic conservation, or it could be a side manifestation of other important characters. Here is an open field for geneticists and physiologists.

Another apparently expanding character in the same frog is the presence in males of external vocal sacs, which is geographically centrally situated in relation to a lack of these sacs. Here it is possible that the frogs with external sacs have a call that is somehow superior. In these days when analysis of frog calls has reached a high degree of refinement, possible variation in the call and breeding system of *Rana pipiens* ought to be looked into.

The legless lizard, *Anguis fragilis* (L.), shows a similar pattern in the distribution of a blue-spotted morph in Europe. This lizard ranges from Persia and the Sahara north to Scotland, Scandinavia and northwestern Russia, but the blue-spotted

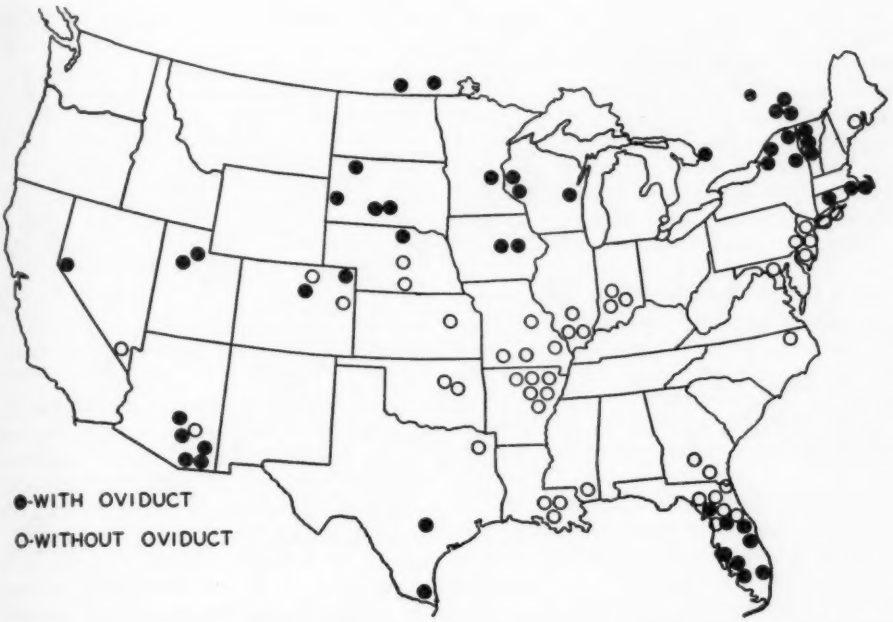

FIG. 1. Distribution of males of the frog *Rana pipiens* in the United States and Canada, plotted by oviduct presence or absence. Each circle or dot represents 1 to 4 frogs dissected; those in Vermont, New Jersey and Long Island represent much larger samples. (After Moore, 1944.)

morph is known only from the central parts of this range, avoiding Scotland, Denmark, the Scandinavian Peninsula proper, and most of France, although in Finland it gets as far north—65°—as the species goes. Functional correlations for the blue spotting are unknown, though other anguid species have it as a regular character (Voipio, 1956, and other sources).

Figure 2 shows the development of long crest feathers in a tropical Asiatic drongo, as mapped by Vaurie (1949). The crest is very long—the specialized condition—on the mainland, and decreases outward toward peripheral islands in several directions. Crest characters in birds often are important in courtship or territorial displays, and it seems safe to extend this reasoning to this particular drongo.

These few cases should serve to illustrate what I mean when I talk about noncorrelated geographical variation. They all cry out for investigation by workers in various disciplines, especially morphology, physiology, genetics, and ethology. In the cases of the frog and bird, I have guessed at possible functional advantages of the presumedly "advanced" characters. These advantages (metabolic conservation, improved efficiency of courtship), even if they do fit the cases cited, would probably not be the whole story by any means. For if metabolic conservation and courtship efficiency are improved, then more frogs or birds will be produced, which only brings up problems of crowding and food supply. Here we may glimpse the complexities of one of the ranking problems of our science: what are the attributes of biological success?

But such characters as external vocal

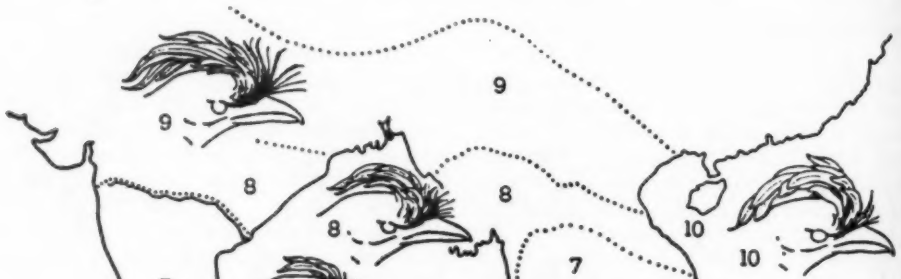

FIG. 2. Variation in the crest of the greater racket-tailed drongo (*Dicrurus assimilis*). The numbers refer to races recognized by Vaurie. Birds from Malaya and southeastern Sumatra (No. 4) are really mostly like the Javanese birds (No. 5). The short-crested type shown for No. 4 is more characteristic of the western Sumatran islands. (After Vaurie, 1949.)

sacs representing (let us suppose) increased courtship efficiency in *R. pipiens* may often tend to be independent of the environment in the sense that they are adaptively positive anywhere the frog can maintain breeding populations. I am not implying that increased reproductive rates are never special-adaptive, for things like sex ratios and number of brood are often geographically variable. But the kinds of changes that spread to all parts of a species range must have some broad general significance in the metabolism, reproduction, behavior or social organization of the animal that makes them adaptive throughout that range. To distinguish them from special-adaptive characters, we may call such characters (or their visible correlates) *general adaptations.*

Although I have been discussing special and general adaptations as though they were absolutely different, I think that in reality they grade completely into one another. Probably no adaptive character reacts with but a single environmental variable, to the exclusion of all others, and it may well be that there exists no adaptation so perfectly general that its value is the same in all environments occupied by the species.

I suppose that many writers have touched upon or implied the distinction between general and special adaptation. The names of Darwin, Matthew, Wright, and Goldschmidt have come up in this connection, but I find the distinctions they make either ambiguous or unsatisfactory in some other way. My own ideas

originated with P. J. Darlington (1948: 109):

> The second kind of evolution, *adaptation to special environments,* is not random; mutations that happen to be advantageous under special conditions are selected. . . . The third kind of evolution is *general adaptation.* It includes all the improvements of organs and functions that allow some animals to live more efficiently than others in many environments, to react more rapidly or more intelligently, or to produce more offspring, or offspring that are more likely to survive. It is adaptation to the general environment of the world, and it should lead to general dominance, to success over great areas and in many special environments.

I feel that even the distinction drawn by Darlington can be stated in a more advantageous way, so as to include conditions existing below the level of the major groups with which he dealt exclusively.

Both at and above species level, special adaptations appear to function to fit the organism or population to the particular features of the immediate environment. General adaptations are concerned more with internal organization and efficiency of the individuals or population, more or less independently of the local details of the environment.

General Adaptation and Radiation

In my paper on centrifugal speciation (1957), I mentioned briefly the importance of general adaptation in speciation, particularly in the origin of "potent" species—those most likely to succeed in leading on to higher categories. In that paper, I did not have quite the same conception of general adaptation as I do at present, for I then included under the concept those improvements that enable a species to extend its range more or less permanently.

In the present idea, such adaptations could conceivably be either special or general. I call them *extension adaptations*; they form an entirely different category that will not be considered here.

But even in the present restricted meaning, general adaptation seems to me to represent one of the potentially more important factors in evolution. The species from which arise new phyletic lines must usually in the long run be among the best generally-adapted ones of their group or genus. Abundant evidence points to special adaptation, at least in its more extreme manifestations, as the mark of evolutionary stagnation or the road to extinction. Many species-groups or genera among the animals seem to have one species that is highly successful and stands apart from the other species in this and other respects; such "potent" species usually are the obvious rapidly evolving ones in the group. Paradoxically, such species often show a majority of traits that are more generalized than those of their congeners.

The Hawaiian drepaniid birds may furnish one illustration. As is well known now from the work of a long succession of investigators (summary by Amadon, 1950), the drepaniids must have arisen from a single stock arriving in the Hawaiian group, probably from the Americas. This stock has given rise to a whole series of species, the extreme forms of which are very different from one another in structure (especially of the head and bill), in plumage and in ecology. At least half the known species are extinct or nearly so. The extinct forms are, in general, structurally among the most highly specialized, and there is reason to believe that they were restricted to rather small ranges and to narrow ecological niches, particularly in their feeding.

By contrast, the forms that are today most abundant, widespread, and ecologically polyvalent—forms like *Loxops virens*—are relatively unspecialized in bill structure and feeding habits. In fact, some writers (e.g., Amadon) believe that a bird much like *L. virens* in general build must have been the original stock from which all drepaniids descended. It is also probably significant that *Loxops virens* shows fairly extensive geographical variation, a fact suggesting continuing ac-

tive evolutionary tendencies in this species.

The evolution of a group of animals like the drepaniids on an oceanic archipelago may proceed about as follows: an original limited stock arrives on one of the islands, establishes, and begins to spread to the other islands. The spread is primarily dependent on density increase in the source population. In birds (including the drepaniids) high density situations may lead to a rather direct type of "flock emigration," in this case to other islands. Similar flights occur among the insects. Many other animals, perhaps most, are carried more or less passively by wind or water, but their exposure to these agencies probably depends to a large extent on their forsaking their native shelter under pressure of high population density. In the course of time, the suitable islands, at least those nearest the source island, are populated.

The largest island with favorable environment, once occupied, becomes the source of the largest populations, and those most likely to originate the best general adaptations (Darlington, 1948, 1957; Brown, 1957). This large island now becomes the main source island. From it issue the main emigrations that populate the other islands. These emigrations are like successive expanding waves, separated by periods of population contraction and isolation, and driven by the force of population density fluctuation.

If one wave differs enough genetically from a preceding wave, reproductive isolation now separates the two as different species when the new-central wave reaches the old-peripheral populations. Once this happens, the two populations are likely thrown into competition for one or more requisites, such as food or shelter. Competition between two closely related species apparently can have only three general outcomes:

1. The two species occupy different areas, and do not interpenetrate one another's ranges.

2. The two species occupy different ecological niches in the areas where ranges overlap.

3. One species is eliminated by aggression or some kind of interference on the part of the other.

These three results are not clearcut, and one may contain elements of the other two; for instance, occupation of different ranges may involve ecological differences and may be enforced through dominating aggression of one of the species.

It is the second result that interests us most, for related species occupying different niches in the same area tend to show special adaptive adjustment that results in their increased structural and behavioral difference in this area. In many cases among animals, the situation arises where differences between close species are seen as clearcut only where their ranges overlap. Brown and Wilson (1956) deal at length with this phenomenon, which we call "character displacement."

Here is Amadon's description of the character displacement between two species of the Hawaiian honeycreepers:

> In the Drepaniidae, the genus *Loxops* presents an instance of speciation by double colonization upon Kauai and adaptive changes in the bill are already perceptible. *Loxops virens* ranges throughout the main islands, while *L. parva* (Stejneger) is restricted to Kauai. The former feeds chiefly upon insects sought among foliage and also, to a considerable extent, upon nectar. Occasionally it hunts upon the boughs of trees for insects, using its bill to tap or pry away bits of bark or lichens. The Kauai race, *Loxops virens stejnegeri* (Wilson), of the widespread species, has a noticeably heavier bill than the races of the other five islands. Munro wrote of *stejnegeri*: "I noted particularly in skinning that the muscles on the back of its head were more strongly developed than in the other Kauai birds and its skull more heavily built. This development was evidently occasioned by its habit of digging in the bark of trees to a greater extent than any of the other Kauai birds; or other amakihis (i.e., other races of *L. virens*)." *Loxops parva*, on the other hand, is a tiny bird, smaller than any race of *L. virens*. It has a small, almost straight bill, very unlike the stout curved one of *stejnegeri*. Of *parva* Munro wrote: "It usu-

ally gathers its insect food among the twigs and leaves but sometimes in the loose bark. It is very fond of visiting the koa flowers." Perkins also contrasted the habits of these two Kauai species and stated that in its manner of digging out concealed insects with its bill *stejnegeri* resembles *Hemignathus lucidus*.

To summarize, on the islands where but one species of this group (*Loxops virens*) occurs, it has generalized feeding habits. On Kauai where two species are present as a result of a double invasion, they have, so to speak, divided the ecological niche of the parental species between them (and extended it). *L. v. stejnegeri* has specialized for securing insects from beneath bark. Its bill has become strengthened by the natural selection resulting from such habits. *Loxops parva* restricts itself almost exclusively to food obtained from foliage and shallow flowers. Thus divergence and incipient specialization have resulted from competition between two similar species. Evidently their needs no longer conflict seriously since both are reasonably common.

As I have suggested elsewhere (Brown, 1958), it is probably usual for a better generally-adapted, new-central population arriving at a peripheral island to take the lion's share of the available niches, while the old resident population is left to make out as best it can by specializing. Thus, as far as special-adaptive characters go, the new-central population remains more like the ancestral population than does the old-peripheral one.

Now, let us imagine this process of population waves, reproductive isolation and ecological displacement repeated time after time. The result of adding a third species-wave to the second is a further narrowing of the niche occupied by the original old-peripheral population, and the second arrival is now also forced to specialize somewhat. As wave after wave arrives, the older populations are pushed into an ever-narrowing ecological corner, which their structural and behavioral specialization must follow. If their environment is stable and remote, they may survive for ages, but for most such specialists, extinction is sure and rapid as new waves arrive in their refuges.

The process I have described is *multiple character displacement*. It is nearly or quite the same thing as *adaptive radiation*, and for purposes of this discussion, I shall consider the two terms synonymous. If we plot an evolutionary sequence to show general-adaptive as well as special-adaptive evolution, it should resemble the phylogenetic diagram of Figure 3. Note that the special-adaptive (radiative) evolution is mainly horizontal, while the general-adaptive axis is vertical, representing change in time.

It seems likely, as Amadon (1950, p. 247) and others have already suggested, that radiative evolution under circumstances such as those postulated for the drepaniids can be extremely rapid. I think it may even be more rapid than Amadon seems willing to allow, though this assumption requires development in a separate paper, and will not be gone into here. But it can be assumed that the really rapid pace of the radiative divergence (displacement) of species occurs during and just after the periods when new species waves overcome the refuges of older ones. In periods between effective waves, we may assume that a sort of balance is reached among the species populations of a given area, and that radiative divergence is thereupon temporarily slowed or even interrupted. Such alternation of evolutionary rates affecting special-adaptive characters may, in fact, pretty much account for what has been called "quantum evolution," "macromutation," or (Schindewolf's) "typostrophe." It may also cover many of the saltatory variations in paleontological sequences that have been laid to "gaps in the geological record," and could just possibly provide a reasonable basis for the objective distinction of chronological species.

General Adaptation and Population Dynamics

It can be seen from the considerations outlined above that the distinction between general and special adaptation may well be a fundamental one, heretofore not widely enough considered in evolutionary

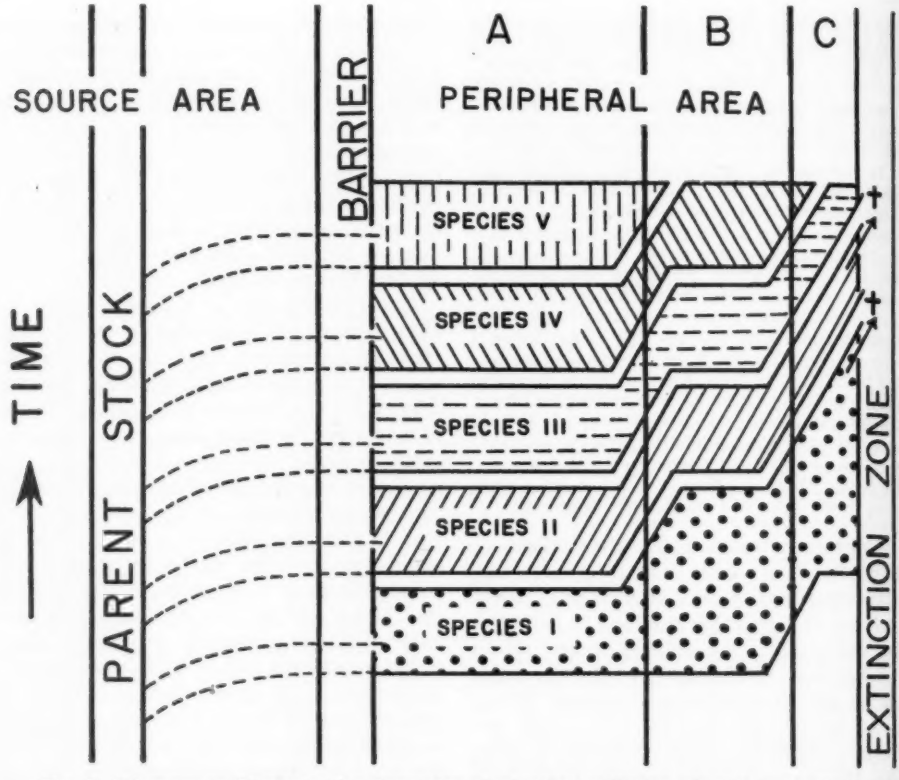

FIG. 3. Diagram to illustrate the dynamics of adaptive radiation viewed as multiple character displacement. To the left of the BARRIER is a SOURCE AREA occupied by a PARENT STOCK which gives rise to successive emigrant species (double dashed lines). As each species moves in turn across the BARRIER into the PERIPHERAL AREA (at right), it displaces any previous occupants from the broadest adaptive zone (A) into narrower adaptive zones (B, C). As species are added to the PERIPHERAL AREA, the more specialized ones are displaced into narrower and narrower zones, and eventually many are pushed into the EXTINCTION ZONE.

thinking. In fact, I think that it may be advantageous for us to view organic evolution from one direction as a process through which general adaptations are created, fostered, and spread. I also think that the role of population dynamics in evolution may have been misunderstood. Now it is becoming clearer that density fluctuation and emigration are "built-in" functions of the population, probably genetically conditioned and subject to natural selection (Lack, 1954; Chitty, 1958). It has been widely assumed that these functions operate primarily as governors, preventing densities from reaching catastrophic extremes that would mean extinction for the population. There is much that is attractive in this point of view. But it seems to me that there is more to be considered. Populations in nature may fluctuate violently, but many apparently do not. It would seem that in many cases, particularly among widespread and successful species, fluctuation

is excessive in amplitude, causing a waste of individuals far beyond what one would think economic in a governance system.

On the other hand, I have the impression that small, isolated populations, particularly of specialized species, tend to maintain relatively stable population densities. Studies of game animals (Leopold, 1933; Graham and Hunt 1958) indicate relative stability (*within single species*) for isolated populations, while some large, continuous, wide-spread populations are prone to fluctuate violently. Comparative data on fluctuation of population density in different species and higher taxonomic groups is much needed, and should not be too hard to get.

Animals of the widespread and successful type, and particularly those that show strong density fluctuation, seem often to possess well-developed morphological and behavioral mechanisms for dispersal. Conversely, the specialized species occurring in peripheral or limited areas—particularly on islands and mountaintops—tend to be more sedentary, and frequently show atrophy of the kind of morphological adaptation needed for wide-scale dispersal movements. Examples of this are the well-known concentration of flightless birds (excepting the few large ratites) on islands (several cases discussed by Greenway, 1958) and of flightless carabid beetles on islands and mountain peaks (Darlington, 1943). An inbred laboratory strain of *Drosophila melanogaster* showed mass-emigration behavior only when its densities reached significantly higher levels than those at which wild-caught strains of the same species began to mass-emigrate, according to Sakai and associates (1958). Here, the laboratory strain represents a specialized population in a stable, restricted environment.

Despite very inadequate information at present, there are nevertheless enough signs to raise the possibility that general adaptation, population density fluctuation, and developed dispersal mechanisms may be causally correlated attributes of "potent" populations. Conversely, it seems possible that special adaptations, population density stability, and obsolescence of dispersal mechanisms may tend to be more characteristic of those populations with relatively limited evolutionary potential.

These circumstances suggest an hypothesis: *Density-dependent population fluctuations and mass-dispersal mechanisms in animals have as a major function the promotion of assembly and spread of general adaptations.* I think that, by and large, this function may be at least as important as the presumed one of density governance.

In this paper so far, I have tried to demonstrate the potential usefulness of distinguishing general adaptation and its role in different phases of the evolutionary process. I have been concerned with general adaptation within single species, and, by later implication, between species. Different aspects of the phenomenon call forth different definitions. For the student of intraspecific geographical variation, emphasis lies chiefly in the distributional aspect of the adaptations. For the ecologist or the paleontologist,[2] the functional aspect holds the greatest interest. Presumably geneticists and physiologists would be engaged more with the content, structure, dynamics and mode of develop-

[2] In the Joint Meetings of the Society for the Study of Evolution and the Society of Vertebrate Paleontology, August 31 to September 5, 1958, at Ann Arbor, Michigan, I read a paper entitled, "The Kinds of Adaptation" that contained a condensed version of the views here expressed. During these same meetings, by complete coincidence, Dr. E. C. Olson read a paper dealing with the reptile-mammal transition, in which he made the same distinction between general and special adaptations above the species level, even using these same terms. I have heard that the same or a similar distinction is also being drawn by some geneticists and ecologists as an aid to interpreting their work in progress. To me, these signs indicate that the time is ripe for closer consideration of general adaptation. See also S. Wright, 1941, Ecology, 22:347.

ment of general adaptations. About these last subjects we can offer a few suggestions even now.

General Adaptation and Breeding Structure

It seems safe to assume that general adaptations are normally based on complex genetic systems. These systems must be assembled from the variability constantly accumulating in all the populations (demes) of the species. The process of assembly necessarily includes genetic recombination. But recombination, to be maximally effective, requires (1) frequent genetic contact among the populations [see Wright, 1956 and earlier papers], and (2) a strongly outbreeding system. Condition (1) should be ideally met by a series of neighboring populations fluctuating in density and able to mass-disperse under pressure of density peaks; I have already discussed this matter above. Condition (2) seems to me to hook up with what we know about breeding-structure types among animal species as related to other aspects of the biology of the species.

Sexual reproduction, as a strong form of outbreeding, is found in all phyla of animals and plants. It appears that it is a primitive characteristic in the evolution of these groups, persisting at least from the Protista and perhaps even from lower acellular forms of life. By contrast, most asexual reproduction and other obligatory strong inbreeding seems to be characteristic of animals which on all evidence are likely ultimate derivatives of sexually reproducing, outbreeding stocks. To exemplify this, I need point only to the evolution of parasitic animals in general. Parasites of widely divergent phyla and orders show a common evolutionary trend toward extreme, rigid specialization, and a more or less parallel tendency to substitute inbreeding (adelphogamic, hermaphroditic, parthenogenetic, etc.) systems for the freer kinds of outbreeding.[3]

[3] Boyden (1954, Syst. Zool. 3:26–37) thinks that asexual reproduction is primitive in the Metazoa, and that sexual reproduction is derivative. However, his argument assumes that the "simplicity" of asexual reproduction infallibly represents a primitive character, whereas systematists find that the most obvious trend in many phyletic lines is toward simplification or reduction.

Among free-living protozoans, Sonneborn (1957) notes that the ciliate genus *Paramecium* contains groups of very closely related species (Sonneborn calls his cryptic species "syngens") that differ markedly in distribution, breeding structure, and life cycle. In general, the species that outbreed appear to be the widely distributed and successful ones, while those at the other extreme of breeding type are mostly rarer and more restricted in range. At present, though, we know practically nothing about the comparative ecology of these species in nature.

The scraps of evidence we have suggest another hypothesis: *Outbreeding is necessary for the maintenance of general adaptation, but becomes superfluous and tends to be lost in species and higher groups in which the emphasis has switched to special adaptation.*

Summary

1. Within single species, geographical variation seems to be correlated with two types of adaptations: *special adaptations*, in which the variation follows particular environmental variables, and *general adaptations*, in which the variation takes up a broad pattern (often centrifugal) independent of environmental differences within the species range.

2. Both at and above species level, special adaptations appear to function to fit the organism or population to the particular features of the immediate environment. General adaptations are concerned more with internal organization and efficiency of the individuals or population, more or less independently of the details of the environment. Of course, the two types of adaptation differ as extremes of emphasis, and not as absolutes.

3. Adaptations that permit a species or

group to extend its range permanently are in a different category, called *extension adaptations*, which may include special and/or general adaptations.

4. Species-groups or genera normally contain one or more potent species in which general adaptation is prominent. The potent species represents a kind of "apical growing point" of general adaptation, and continues the line most likely to give rise to new major groups.

5. The "lateral" component in evolution is represented by the more specialized species of the group. The differences between these are primarily due to *adaptive radiation* based on repeated *character displacement*.

6. Character displacement proceeds most rapidly at the first contact of the mutually-displacing species, and later slows down as the species reach equilibrium among themselves. The resulting disparity in rates of divergence may account in large part for the discontinuity ("saltations") in the paleontological record, and may provide a basis for more objective separation of chronological species.

7. It is suggested that density-dependent population fluctuations and mass-dispersal mechanisms in animals have as a major function the promotion of assembly and spread of general adaptations.

8. Outbreeding is necessary for the maintenance of general adaptation, but becomes superfluous and tends to be lost in species and higher groups in which the emphasis has switched to special adaptation. This may account in large part for the degeneration of outbreeding in so many parasitic animals.

LITERATURE CITED

AMADON, D. 1950. The Hawaiian Honeycreepers (Aves Drepaniidae). *Bull. Amer. Mus. Nat. Hist., 95*:151–262.

AUFFENBERG, W. 1955. A reconsideration of the racer, *Coluber constrictor*, in the eastern United States. *Tulane Stud. Zool., 2*:87–155, *cf.* 108.

BENSON, S. B. 1933. Concealing coloration among some desert rodents of the southwestern United States. *Univ. Calif. Publ. Zool., 40*:1–70.

BROWER, L. P. 1958. Bird predation and foodplant specificity in closely related procryptic insects. *Amer. Nat., 92*:183–187.

BROWN, W. L., JR. 1957. Centrifugal speciation. *Quart. Rev. Biol., 32*:247–277.

——— 1958. Some zoological concepts applied to problems in evolution of the hominid lineage. *Amer. Scientist, 46*:151–158.

BROWN, W. L., JR., and WILSON, E. O. 1956. Character displacement. *Syst. Zool., 5*:49–64.

CHITTY, D. 1958. Self-regulation of members through changes in viability. Population studies: animal ecology and demography. *Cold Spring Harbor Symp. Quant. Biol., 22*:277–280.

DARLINGTON, P. J., JR. 1943. Carabidae of mountains and islands: Data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monogr., 13*:37–61.

——— 1948. The geographical distribution of cold-blooded vertebrates. *Quart. Rev. Biol., 23*:1–26, 106–123.

——— 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, New York, 675 pp.

GREENWAY, J. 1958. Extinct and vanishing birds of the world. Amer. Comm. Internat. Wild Life Protection, New York, 518 pp.

GRAHAM, S. A., and HUNT, G. S. 1958. A noncyclic ruffed grouse population near Ann Arbor, Michigan. *Jour. Wildlife Management, 22*:427–432.

HAMILTON, T. 1959. Adaptive variation in the genus Vireo. *Wilson Bull., 70*:307–346.

HUXLEY, J. 1943. Evolution: the modern synthesis. George Allen and Unwin, Ltd., London, *cf.*, pp. 206–227.

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, New York and London, 343 pp.

LEOPOLD, A. 1933. Game-management. Charles Scribner's Sons, New York, *cf.* Chapter 3.

MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York, *cf.*, pp. 88–94.

MOORE, J. A. 1944. Geographic variation in *Rana pipiens* Schreber of eastern North America. *Bull. Amer. Mus. Nat. Hist., 82*: 345–370.

——— 1949. Geographic variation of adaptive characters in *Rana pipiens* Schreber. *Evolution, 3*:1–24.

NIETHAMMER, G. 1940. Die Schutzanpassung der Lerchen, *in* Hoesch and Niethammer, Die Vogelwelt Deutsch—Suedwestafrikas. *Jour. Ornith, 88* (Sonderh.): 75–83.

SAKAI, K., NARISE, T., HIRAIZUMI, Y. and IYAMA, S. 1958. Studies on competition in plants and animals. IX. Experimental

studies on migration in Drosophila melanogaster. *Evolution, 12*:93–101.

SONNEBORN, T. M. 1957. Breeding systems, reproductive methods, and species problems in Protozoa. In The Species Problem, ed. E. Mayr, Amer. Assoc. Adv. Sci., Washington, *cf.*, pp. 155–324.

VAURIE, C. 1949. A revision of the bird family Dicruridae. *Bull. Amer. Mus. Nat. Hist., 93*:199–342.

VOIPIO, P. 1956. On the blue-spotted morph of the slow-worm (*Anguis fragilis*) in Finland. *Arch. Soc. 'Vanamo,'* Helsinki, *11*:5–11.

WRIGHT, S. 1956. Modes of selection. *Amer. Nat., 90*:5–24.

WILLIAM L. BROWN, JR. is Associate Curator of Insects in the Museum of Comparative Zoology at Harvard College. For useful suggestions and criticism, he is grateful to P. J. Darlington, Jr., A. V. Grimstone, A. J. Meyer-riecks, R. Milkman, B. Patterson, E. E. Williams, and E. O. Wilson. For permission to use illustrations, he is indebted to J. A. Moore and C. Vaurie. Of course, their acknowledgement is not meant to imply that they necessarily endorse the views here put forward.

Are There Rodent Suborders?

ALBERT E. WOOD

THE rodents are the most numerous order of mammals, both in terms of genera and species, and of individuals, including over half of the described living species of mammals. They are much less well represented among the known fossils, but this is, to a very large extent, the result of their small size and hence lesser conspicuousness, rather than of a former lesser diversification, at least since the latter part of the Eocene. The basic characteristic of the order—the development of gnawing incisors—has restricted the number of ecologic niches that were open to rodents. Since rodents have become very successful in this limited direction, many lines have developed, tending to evolve in the same general direction, due to similar selective pressures acting on a similar genotype. This has produced a great deal of parallelism and convergence within the order, as is now acknowledged by all students of the group.

Due to this parallelism and convergence, one is faced with the problem of differentiating between similarities indicative of close relationships and those that are not. Hence, there has been, and still is, considerable difference of opinion as to the proper classification of the order. The classical arrangement, involving a subdivision into the Sciuromorpha, Myomorpha and Hystricomorpha, fundamentally on the basis of the structure of the masseter muscle, dates from Brandt (1855), although similar but less formal arrangements had been proposed before. Simpson (1945) is the latest major review of classification to adopt this three-fold arrangement. Although this has been the standard classification, many investigators felt (as, indeed, did Simpson) that its use involved forcing some rodents into unnatural relationships for purposes of convenience. Therefore, greater or lesser variants were proposed (Tullberg, 1899; Miller and Gidley, 1918; Winge, 1924). Tullberg's scheme divided the rodents into two major groups, based on the structure of the angle of the jaw, and then divided each of these on the basis of the masseter. For his secondary divisions, he used Brandt's three groups, erecting a fourth group for the South African Bathyergidae. Neither Winge nor Miller and Gidley use Brandt's terminology, but, essentially, accepted his groups and added a fourth for the forms which did not fit well into this scheme. These fourth, or "wastebasket," groups have never met with wide acceptance.

Even in cases where the suborders seemed morphologically valid, parts of the Brandtian classification seemed unreasonable to some authors. For example, the Hystricomorpha included certain Old World (particularly African) families, and a large array of South American ones, which were assumed to be of ultimate Old World origin. For many years, this was interpreted as indicating a South Atlantic land bridge. With increasing knowledge of the character and distribution of fossil mammals, no such land bridge seemed possible as an invasion route for the South American rodents (Simpson, 1950), and the problem of the origin of the South American forms became a major stumbling block in accepting the unity of the Hystricomorpha. Wood (1950), in view of the known extensive parallelism among rodents, suggested that the similarities between the New and Old World forms could best be explained as parallelisms, and that the source of the South American forms should be sought in North America.

Within the past few years, there has

been a growing feeling among students of rodent evolution (Lavocat, Schaub, and Wood) that all the classic suborders are unnatural groups, resulting in a number of rather diverse classifications, although all agree in eliminating or highly modifying Brandt's classic suborders (e.g., Lavocat, 1951; Schaub, 1953*a;* Viret, 1955; Wood, 1955).

All of these authors, however, have had one basic assumption in common—the desirability of presenting a classification that would fit all rodents into subordinal groups. This resulted, at one extreme, in the division of the rodents into but two suborders by Kretzoi (1943), and at the other in the separation of the order into seven suborders by Wood (1955), which, as pointed out by Wood and Patterson (1959), following the suggestions of Lavocat (1956, p. 52-53), should perhaps be increased to as many as eleven. This multiplicity is based on separating all forms whose probable relationship has not yet been demonstrated. Many of these eleven suborders would be of very small size, containing only one or two families (see left hand column of Table I).

There is, however, an alternative approach which has many advantages. If the rodents are analyzed, there are certain groups of families that are clearly related, and which all authors agree to be related, whatever taxonomic level these groups are considered to represent. In other cases, there is a wide diversity of opinion as to the relationships of the families concerned, some not appearing to have any near relatives. What I should like to suggest is the possibility that this situation is not merely an indication of current imperfect knowledge, but that it may represent a true picture of rodent phylogeny and relationships.

The Protrogomorpha, a suborder including a series of extinct families (the Eocene and Oligocene Paramyidae, Sciuravidae, Cylindrodontidae, Protoptychidae, Ischyromyidae and probably Phiomyidae; the mid-Tertiary Mylagaulidae; and the Miocene to Recent Aplodontidae) seems surely to be a natural group, embodying the primitive members of the order, as well as some of their less divergent derivatives, all being characterized by a very restricted use of the masseter muscle, which resulted in inefficient gnawing as compared with more advanced forms.

Another natural group is the Caviomorpha, a term proposed by Wood and Patterson (*in* Wood, 1955; Wood and Patterson, 1959) for the South American "hystricomorphs" including the Octodontidae, Echimyidae, Ctenomyidae, Abrocomidae, Capromyidae, Chinchillidae, Dasyproctidae, Cuniculidae, Heptaxodontidae, Dinomyidae, Eocardiidae, Caviidae, Hydrochoeridae, and Erethizontidae. Whatever one may think about the justification for making this a suborder distinct from the Old World "hystricomorphs," all authors agree that it is a natural group, and most are in accord that it represents the descendants of a single form that invaded South America.

As revised by Wood (1955), following suggestions by Wilson (1949) and Schaub (1953*b*), the suborder Myomorpha includes nine to eleven families that had been placed in various positions by other authors. As Wood has recently suggested (1959), it seems quite possible that this suborder is polyphyletic, having been derived on three to five independent occasions from what seems very probably to have been a closely related group of protrogomorphs. This means that, if a suborder is to be treated as a phyletic unit, originating from a single source, either the protrogomorph ancestors would have to be shifted to the Myomorpha (as has been suggested, though not in just these words, by Schaub, *in* Stehlin and Schaub, 1951, p. 336), or the Myomorpha would not be considered a valid unit. On the other hand, recent discussions of the polyphyletic origins of teleosts, amphibians, reptiles, and mammals shows that most students do not feel that the probability

of a multiple origin from a closely related ancestral stock requires the splitting of useful taxa.

This suggested polyphyletic origin of the Myomorpha, however, provides a clue as to what may well have been the probable phylogenetic development of the rest of the order. As already mentioned, the Protrogomorpha were relatively poor gnawers. During the middle and later Eocene, many members of this group began to develop a more powerful anteroposterior movement of the lower jaw in gnawing, brought about by the forward growth of the masseter muscle onto the snout. There were only a limited number of ways in which this migration of the masseter could have developed, and the selection for this growth must have been strong, as soon as such movement had begun. For this reason, there was a great evolutionary burst among the rodents, toward the end of the Eocene, which apparently occurred in all parts of the world where there were rodents. It seems almost certain that, in this burst, a great many protrogomorphs gave rise to non-protrogomorph lines. At the present time, we know very little about the protrogomorphs except from Western North America, but a few are known from Europe, Asia, and Africa, and our poor knowledge of the Eocene of much of the Old World permits the assumption that they may have been present in parts of these continents in a diversity as great as in North America.

Subsequent evolution of these non-protrogomorph lines was undoubtedly varied. Some, such as the Sciuridae, became successful and nearly world-wide in their distribution. Others were less successful, and presumably many died out without having left any record that has yet been uncovered. It is the thesis of the present paper that, although our current inability to group some of these lines may be due in part to our very limited knowledge of the Tertiary rodents of Africa, to which continent a number of families are restricted, nevertheless many of the families or superfamilies of rodents that have proved very difficult to place subordinally may prove to have had independent origins from the protrogomorphs.

If this interpretation is correct, the most accurate picture of the true rodent phylogeny might agree with the most accurate picture of our current knowledge of the subject—namely the division of the order into three large groups of families, which should surely be called suborders; three or four small groups of families, which are clearly superfamilies; and six independent families. It is undoubtedly true that some of these independent families and superfamilies may ultimately be shown to be derived from common or closely related protrogomorph ancestors, at which time they should be grouped into suborders. But, for the present, this is impossible.

We are, therefore, faced with three alternatives for the classification of the rodents, if these interpretations of the meaning of the evidence are correct:

(1) We could accept the groups here called Protrogomorpha, Myomorpha, and Caviomorpha as valid suborders, using either these names or others, and assign all remaining rodents either to these or to one or more frankly wastebasket suborders;

(2) We could accept the three main suborders, and establish a new subordinal name for each of the families or superfamilies of unknown or uncertain relationships; or

(3) We could accept the three suborders, and leave all the remaining groups as independent families or superfamilies until some other relationships have been established.

The first of these possibilities is the best for the non-specialist because it provides a simple and easily understood classification, with a very limited number of major groups. It has the disadvantage, however, that it would be

TABLE I—Comparisons of Two Possible Approaches to Rodent Classification

I. ALL RODENTS IN SUBORDERS	II. HIGHER TAXONOMIC UNITS ONLY WHEN REASONABLY WELL AUTHENTICATED
Suborder Protrogomorpha	Suborder Protrogomorpha
Superfamily Ischyromyoidea	Superfamily Ischyromyoidea
Paramyidae, Sciuravidae, Cylindrodontidae, Protoptychidae, Ischyromyidae, Phiomyidae	Paramyidae, Sciuravidae, Cylindrodontidae, Protoptychidae, Ischyromyidae, Phiomyidae
Superfamily Aplodontoidea	Superfamily Aplodontoidea
Aplodontidae, Mylagaulidae	Aplodontidae, Mylagaulidae
Suborder Caviomorpha	Suborder Caviomorpha
Superfamily Octodontoidea	Superfamily Octodontoidea
Octodontidae, Echimyidae, Ctenomyidae, Abrocomidae, Capromyidae	Octodontidae, Echimyidae, Ctenomyidae, Abrocomidae, Capromyidae
Superfamily Chinchilloidea	Superfamily Chinchilloidea
Chinchillidae, Dasyproctidae, Cuniculidae, Heptaxodontidae, Dinomyidae	Chinchillidae, Dasyproctidae, Cuniculidae, Heptaxodontidae, Dinomyidae
Superfamily Cavioidea	Superfamily Cavioidea
Eocardiidae, Caviidae, Hydrochoeridae	Eocardiidae, Caviidae, Hydrochoeridae
Superfamily Erethizontoidea	Superfamily Erethizontoidea
Erethizontidae	Erethizontidae
Suborder Myomorpha	Suborder Myomorpha
Superfamily Muroidea	Superfamily Muroidea
Cricetidae, Muridae	Cricetidae, Muridae
Superfamily Spalacoidea	Superfamily Spalacoidea
Spalacidae, Rhizomyidae	Spalacidae, Rhizomyidae
Superfamily Geomyoidea	Superfamily Geomyoidea
Geomyidae, Heteromyidae, Eomyidae	Geomyidae, Heteromyidae, Eomyidae
Superfamily Dipodoidea	Superfamily Dipodoidea
Dipodidae, Zapodidae	Dipodidae, Zapodidae
Perhaps new suborder, perhaps Myomorpha	Perhaps new suborder, perhaps Myomorpha
Superfamily Gliroidea	Superfamily Gliroidea
Gliridae, Seleveniidae	Gliridae, Seleveniidae
	GROUPS NOT ALLOCATED TO SUBORDERS
Suborder Sciuromorpha	
Sciuridae	Family Sciuridae
Suborder Castorimorpha	Superfamily Castoroidea
Castoridae	Castoridae
Eutypomyidae	Eutypomyidae
Suborder Theridomorpha	Superfamily Theridomyoidea
Theridomyidae	Theridomyidae
Pseudosciuridae	Pseudosciuridae
New Suborder	
Ctenodactylidae	Family Ctenodactylidae
New Suborder	
Anomaluridae	Family Anomaluridae
Pedetidae	Family Pedetidae
Suborder Hystricomorpha	
Superfamily Hystricoidea	
Hystricidae	Family Hystricidae
Superfamily Thryonomyoidea	Superfamily Thryonomyoidea
Thryonomyidae	Thryonomyidae
Petromuridae	Petromuridae
Suborder Bathyergomorpha	Family Bathyergidae
Bathyergidae	

strongly opposed by all students of the evolution of the order.

The second possibility combines the advantages of expressing the current knowledge of the order and of providing subordinal pigeon holes for all rodents. It would be, however, cumbersome, with at least ten or eleven suborders, and many of these might be subject to extensive change as further knowledge of the phylogeny of the rodents was accumulated.

The third possibility is the most satisfactory expression of current knowledge, but has the serious disadvantage that it leaves many families with no subordinal assignment, which would be contrary to the goals of formal taxonomy.

A comparison of the second and third possibilities is shown in Table I.

In summary, it is suggested that the present situation, where there are a considerable number of families of rodents that seem to be taxonomically isolated, may be an actual expression of a basic fact in rodent evolution, and that these small groups may never have had a major importance, and have common ancestors only within the primitive suborder, the Protrogomorpha. The question is raised as to how best to express our current knowledge, taxonomically.

LITERATURE CITED

BRANDT, J. F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. *Mém. Acad. Imp. Sci. St.-Pétersbourg,* ser. 6, *9*:1–375.

KRETZOI, M. 1943. Ein neuer Muscardinide aus dem ungarischen Miozän. *Föld. Közlöny, 73*: 271–273.

LAVOCAT, R. 1951. Révision de la faune des mammifères Oligocènes d'Auvergne et du Velay. Paris: *Editions "Sciences et Avenir"*:1–153.

——— 1956. Rèflexions sur la classification des rongeurs. *Mammalia, 20*:49–56.

MILLER, G. W., and GIDLEY, J. W. 1918. Synopsis of the supergeneric groups of rodents. *Jour. Washington Acad. Sci., 8*:431–448.

SCHAUB, S. 1953*a*. Remarks on the distribution and classification of the "Hystricomorpha." *Verh. Naturf. Ges. Basel, 64*:389–400.

——— 1953*b*. La trigonodontie des rongeurs simplicidentés. *Ann. de Paléont. 39*:29–57.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist., 85,* 350 pp.

——— 1950. History of the fauna of Latin America. *Amer. Scientist, 38*:361–389.

STEHLIN, H. G., and SCHAUB, S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweiz. Palaeont. Abhandl., 67*:1–385.

TULLBERG, T. 1899. Ueber das System der Nagethiere: eine phylogenetische Studie. *Nov. Act. Reg. Soc. Scient. Upsala,* ser. 3, *18*:1–514.

VIRET, J. 1955. Rodentia fossiles. La denture des rongeurs actuels et fossiles. Traité de Zoologie. Anatomie, Systématique, Biologie, edited by P.-P. Grassé. Masson et Cie., Paris, *17,* pt. 2: 1526–1564.

WILSON, R. W. 1949. Early Tertiary rodents of North America. *Carnegie Inst. Washington, Publ. 584*:67–164.

WINGE, H. 1924. Pattedyr-Slaegter. Vol. 2. Rodentia, Carnivora, Primates. Copenhagen, H. Hagerups Forlag, 321 pp.

WOOD, A. E. 1950. Porcupines, paleogeography and parallelism. *Evolution, 4*:87–98.

——— 1955. A revised classification of the rodents. *Journ. Mammalogy, 36*:165–187.

——— 1959. Eocene radiation and phylogeny of the rodents. *Evolution, 13,* in press.

WOOD, A. E., and PATTERSON, B. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bull. Mus. Comp. Zool.* Harvard, *120*:279–428.

ALBERT E. WOOD is Professor of Biology, Amherst College, Amherst, Massachusetts. The work reported on here was assisted by grants from the National Science Foundation.

An Analysis of A Sample of Systematic Literature, 1758 to 1954

DONALD J. REISH

THE primary purpose of this subject analysis is to determine whether or not the production of papers in the field of systematics, as indicated by the literature of polychaetous annelids, is increasing or decreasing with reference to the past. Coincident to this, analyses are made with regard to the production of papers by countries and the language employed. Apparently no literature analysis on systematic zoology exists.

Since the principles of scientific nomenclature began with Linnaeus in 1758, there has been a total of 2389 papers through the year 1954 on the systematics of polychaetes. Systematic papers are herein considered to include descriptions of new species, faunistic reports, and monographic studies; excluded are papers dealing with development, physiology, ecology, etc. The basis of this literature analysis was the bibliography of the polychaetous annelids through 1950 which was compiled by Hartman (1951). Ref-

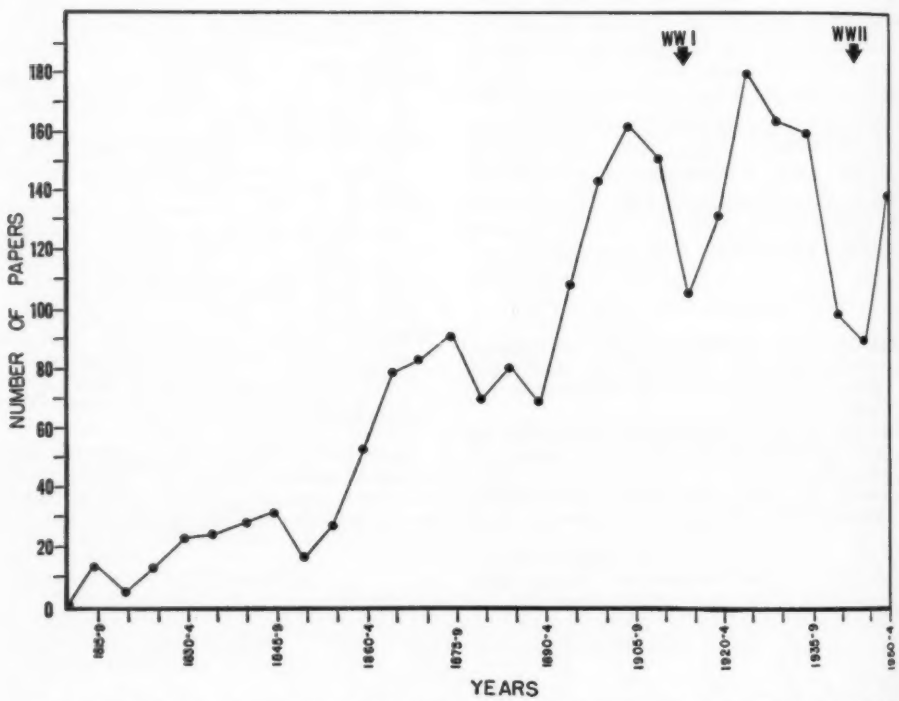

FIG. 1. The output of systematic polychaete literature from 1810 to 1954. Data totaled for five-year periods.

erences since this date were obtained from Zoological Record, Biological Abstracts, and the Russian Biological Abstracts. The data have been totaled by five-year periods and are presented in Figures 1 and 2 and Tables 1 and 2.

Number of Papers

The data for the number of papers written per five-year interval from 1810 to 1954 have been included in Figure 1. Since there were so few papers prior to 1910, these data were excluded from Figure 1. As seen from the curve in Figure 1, there has been a general increase in the number of papers since 1810 with the greatest number, 179, appearing in the 1925–29 period.

Four decreases are noted, two of them corresponding to the two world wars of this century and two occurring during the last century. The cause of these two earlier decreases is not known; perhaps they are due to the greater number of political changes or wars at these times than at other times. World War II had a greater effect on the appearance of systematic papers than World War I; a decrease of 44 percent occurred from World War II as compared to 30 percent from the first one.

It is significant that the production of papers following World War II has not yet reached the peak obtained during the 1925–29 period. It took ten years following World War I to reach and surpass the

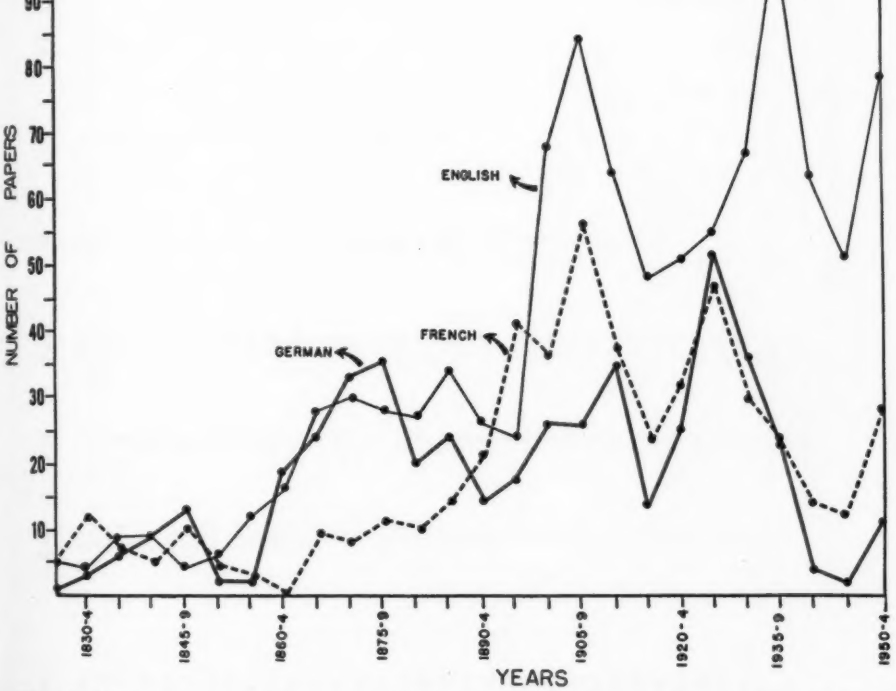

FIG. 2. The number of systematic polychaete papers arranged according to the three important languages employed from 1825 to 1954. Data totaled for five-year periods.

TABLE 1—Number of Papers by Country

YEAR	U. S.	ENGLAND	FRANCE	GERMANY	RUSSIA	ITALY	DENMARK	SWEDEN	JAPAN	NORWAY	NETHER-LANDS	OTHERS
1758–1799		3	3		3	1	10	6		4	3	
1800–4		1	5			1						
1805–9			1				2					
1810–4			1									
1815–9		4	6	5								
1820–4		1	1	2		2						
1825–9		5	5	1		3						
1830–4		4	12	3	2					1		
1835–9		9	5	6						1		
1840–4	1	8	4	6		3	4	3				
1845–9		9	10	8		3	2			1		
1850–4	1	5		4			1			2	2	2
1855–9	6	5	2	5		1	1	5		2		1
1860–4	5	9	1	18		5	2			9	2	2
1865–9	2	19	13	25	1	2	1	8		1		1
1870–4	12	14	8	33	4	2		1		6	1	2
1875–9	9	14	10	36	4	4	4	2		4	2	2
1880–4	14	7	10	18	4							1
1885–9	9	14	12	28	1	1	2	1		5	4	4
1890–4	6	15	19	15	2	3	1	1		1		3
1895–9	6	14	42	16	8	3		7		3	1	4
1900–4	25	31	36	21	1	5	1	3	6	2	1	1
1905–9	24	34	48	24	1	8	1	3	2	3	8	4
1910–4	10	39	36	29	2	9	3	7	3	1	4	5
1915–9	17	10	23	10	2	2	3	5	1		16	15
1920–4	22	17	31	17	7	1	1	6	4		10	12
1925–9	17	24	41	37	20	4	5	5	3	1	1	13
1930–4	16	23	25	29	14	6	4	1	20	3	1	18
1935–9	30	26	22	16	5		8	3	24	2	2	15
1940–4	31	8	10		2	3	5	4		2		32
1945–9	17	5	9	2	5	6	5	1	2	5		27
1950–4	27	14	25	11	8	6	6	2	6	1		30
Totals	207	391	476	436	96	84	77	75	71	60	58	194

Totals	207	391	476	436	96	84	77	75	71	60	58	194

TABLE 2—Number of Papers by Language

YEAR	ENGLISH	FRENCH	GERMAN	RUSSIAN	LATIN	ITALIAN	SPANISH	SWEDISH	NOR-WEGIAN	DANISH	DUTCH	JAPANESE	OTHER
1758–1799	5	3	4		18	1		1	2	1			
1800–4	1	5				1							
1805–9	1												
1810–4		1											
1815–9	4	6	5										
1820–4	1	1			4								
1825–9	5	5	1		3								
1830–4	4	12	3						2				
1835–9	9	7	6						1				
1840–4	9	5	9		4	1		1					
1845–9	4	10	13		1	2			1	2			
1850–4	6	4	2		2				1	1			
1855–9	12	3	2		4	1		4	1	1			
1860–4	16		19			5			9	2			
1865–9	28	9	25	1		3		11	2				
1870–4	30	8	33	4	1	2		1	5		1		
1875–9	28	11	35	3		4			5	3	2		
1880–4	27	10	20	1	3				5	2	1		
1885–9	34	14	24		1	1		1	1	3	1		
1890–4	26	21	14	1		3		1	2	1			
1895–9	24	41	18	7	1	3		4	4		1		1
1900–4	68	36	26	1		5		1	2	1			4
1905–9	85	56	26	2		9	2	1	2		2		1
1910–4	64	37	35	1		7	2	1				2	
1915–9	48	23	14	2		2	10			2	1	1	
1920–4	51	32	25	2		1	4				6	1	
1925–9	55	47	52	8		4	5		1	2			3
1930–4	67	30	36	9		5	4		3	3	1		2
1935–9	99	24	23	4	1		2		1		1		1
1940–4	63	14	4	1		4	11		2				1
1945–9	51	12	2	5		7	8	1	3				
1950–4	79	28	11	8		6	1						1
Totals	1004	515	487	60	45	76	49	27	55	24	17	4	14

former peak. If this holds true for the post-World War II period, then the number of papers appearing during the 1955–59 period should surpass the peak of 1925–29.

Production of Papers by Countries

Since 1758 countries producing systematic papers (Table I) dealing with polychaetes have been, in order of their importance, France (20%), Germany (18.2%), England (16.3%), United States (8.7%), Russia (4%), Italy (3.5%), Denmark (3.4%), Sweden (3.1%), Japan (2.9%), and Norway (2.5%).

Prior to World War I, at least 50 percent of the papers dealing with this subject were written in England, France and Germany. Since that time, 50 percent or more of the papers have been produced by these three countries and the United States, with the exception of the immediate post-World War II period when the three European countries' output was small (Table 1).

The Germans were the most frequent leaders in the productivity of papers during the nineteenth century (Table 1), with the English and French leading during short periods. France emerged as a leader in the production of systematic polychaete papers at the close of the last century. It continued to lead, with the exception of 1910–14, until just prior to World War II. The United States became the leader during the 1935–39 period, a position which it has since maintained. England has never been a leader for any period of time; it has, however, been producing fairly consistently since 1820.

Language

Considering the total number of systematic polychaete papers, English (42.3%) has been the most important language followed by French (21.7%), German (20.5%), Italian (3.2%), Russian (2.5%), Norwegian (2.3%), Spanish (2.1%), Latin (1.9%), Swedish (1.1%), and Danish (1.0%). English emerged as the most important language at the turn of the twentieth century (Fig. 2). During the last century English, French, and German fluctuated as the most important language.

The rise of English may be attributed to several factors. Chief among these has been (1) the increase of papers written in the United States during this century, (2) the first appearance of papers written by the Japanese, who generally used English, at the turn of the century, and (3) the use of English in the Scandinavian countries more frequently than their native languages. Most of the papers written in French and German have been written by natives in those countries.

Latin was the dominant language of the eighteenth century (Table 2), but it has not been an important language since that time.

Discussion

In answer to the question of whether or not the literature of systematic zoology, as indicated by the number of papers dealing with polychaetes, is increasing or decreasing, the post-war production of work has not yet reached the peak attained during the 1925–29 period. Probably this peak will be reached or surpassed during the 1955–59 period. The greatest number of systematic papers written in the United States during any of the five-year periods was attained during the period of 1935–39; this peak will probably be surpassed during the period of 1955–59. Recovery of England, France, and Germany to former peaks has been slower and peaks reached during the 1925–29 period may not be attained for 5 to 10 years from now.

Recently Wesenberg-Lund (1957) published the bibliography of the Gephyrea since 1920. Analysis of the number of systematic papers showed marked similarities to the polychaete literature. A peak of 22 papers occurred during the 1920–24 period and a minimum of 8 occurred during the 1945–49 period. The peak of 22

papers will probably be surpassed in the 1955–59 period.

In the absence of any literature subject analysis in zoology, comparisons have been made with the fields of chemistry and geology. In organic chemistry the numbers of papers surpassed the pre-war peak of 1938 in 1948 (Boig and Howerton, 1952). The number of papers in North American geology had nearly attained the pre-war level by 1948 (Emery, 1951). In general chemistry the pre-war peak had not been reached by the year 1948 (Crane, 1948, 1949).

Comparisons of polychaete systematic literature with other fields of science are more striking when the number of papers of the pre-World War I period are compared to the pre-World War II period. Chemical publications quadrupled from 1909 to 1939; geological publications in North America doubled during this same time; but there was only a 110 percent increase in polychaete systematic literature from the 1905–09 to the 1925–29 period (a slight decrease would be noted if the 1935–39 period was employed). Systematic zoological literature has not maintained the growth that has occurred in these other fields.

Comparisons of production of papers on polychaetes and organic chemistry by countries show some similarities. The five leading countries today are the same, only the order of occurrence is different. United States is the leader of both fields, followed by England, Russia, France, and Germany in organic chemistry (compare with Table 1). Germany dominated the field of organic chemistry until it was surpassed by the United States about 1927 (Boig and Howerton, 1952). The United States became the leader in the production of polychaete systematic papers in 1935–39; France had been the leader from 1895–99.

As stated above, English has been the dominant language employed in polychaete literature since 1900, and for brief periods earlier (Fig. 2). However, it was not until 1927 that English replaced German as the principal language in organic chemistry (Boig and Howerton, 1952). French, Russian, and Italian constitute the other important languages in both fields today.

Summary

Analysis of the systematic literature of polychaetous annelids since 1758 was made of the number of papers, the country of origin, and the language used. Chemical publications quadrupled during the 30 years following 1909; North American geological papers doubled; but only a slight increase occurred from 1909 to the peak years of 1925–29 in polychaete systematic literature.

REFERENCES

Boig, F. S., and Howerton, P. W. 1952. History and development of chemical periodicals in the field of organic chemistry: 1877–1949. *Science, 115*:25–31.

Crane, E. J. 1948. Postwar distribution of scientific research activity. *Jour. Chem. Engn. News, 26*:3342–3343.

——— 1949. Chemical Abstracts. *Jour. Chem. Engn. News, 27*:529–530.

Emery, K. O. 1951. Trends in literature of sedimentology. *Jour. Sed. Petrology, 21*: 105–108.

Hartman, O. 1951. Literature of the polychaetous annelids, vol. I. Bibliography. Los Angeles, California, 290 pages.

Wesenberg-Lund, E. 1957. Sipunculoidea and Echiuroidea from West Africa together with a bibliography on Gephyrea after 1920. *Bull. Inst. Roy. Sci. Nat. Belgique, 33*(42): 1–24.

DONALD J. REISH, of the Biology Department of Long Beach State College, Long Beach, California, is a taxonomic specialist on polychaetous annelids, and has also worked on the effect of pollution on these worms.

Points of View

Problems of Higher Classification

In recent papers Michener and Sokal (1957), Sokal and Michener (1958), and Sneath (1957 *a,b*) have taken pioneering steps in a long overdue quantification of systematic relationships. In subsequent papers Michener (1957) considers problems brought into focus by the quantitative studies, and Inger (1958) attacks the quantitative methodology. These last two papers seem to require further comment. Since an understanding of the problems presented by the so-called weighted variable group (WVG) method of Michener and Sokal will help to clarify the discussion of Inger's views, Michener's paper will be considered first.

Classification and Quantification

Michener emphasizes the fact that there are two types of natural relationships upon which a formal classification can be based. One is the static [1] relationship in which the organisms (evolutionary products) are grouped according to the degree of resemblance (or, conversely, difference) among them. The other is the phyletic classification, in which the temporal factor (recentness of common ancestry) is considered alone. As Bigelow (1956) pointed out, these two schemes are not necessarily compatible. It is clear that a biologist must be interested in both rate and time in evolution; it is not clear which of the two non-compatible schemes should be used as the basis of the formal classificatory hierarchy.

Michener takes the position, with serious reservations and largely on historical grounds, that we should base our formal classification on the presumed phylogeny of the group in question. However, he emphasizes the advantages of static relationships as a basis for classification and urges systematists to state on which type of relationships their classifications are based. Since the ideal of the phylogenetic classification has long been under fire by certain systematists who object to an evolutionary basis of classification, there is some justification for retaining the emphasis on the phyletic system rather than making a move which might be misconstrued as a retreat to classification by essential nature (or some such).

However, in the view of the present author, the advantages of employing the static relationships alone as the basis of formal classification are so overwhelming as to preclude any consideration of the phyletic classification. One of the strongest arguments in favor of the former is that the data which are necessary for arriving at static relationships are almost always available (albeit often difficult to extract), while in most groups the information on phylogeny (e.g., an adequate fossil record) is not available and quite likely will never be available. It should be remembered that many "phylogenetic trees" in the literature would, in more refined terminology, be referred to as diagrams of static relationships.

A second powerful argument in favor of using static relationships is that the information communicated by a nomenclature based on them is, in many cases, more meaningful than that communicated

[1] The term static, while correctly descriptive of the situation, seems to have a somewhat anti-evolutionary connotation to some people because evolution is a dynamic process. The degrees of difference among genotypes might be called evolutionary distances (being evolutionary rate × time), and these distances are static at any given time.

by a nomenclature based on phyletic relationships (only, of course, in cases where the two systems are non-compatible). Perhaps the best known case is that cited by Bigelow. The birds evolved quite rapidly from the archosaurian reptiles. They are more closely related to the crocodiles phyletically than the crocodiles are related to the lizards. However, the crocodiles and lizards are certainly more closely related to each other statically than either is to birds. Adopting a phyletic base, we would be forced to erect the "Birdtilia" (birds, crocodiles etc.) as a group separate from the "Eureptilia." It seems evident that the information conveyed by placing an organism in one of these categories would rarely be as useful as that conveyed by saying that it was a member of the class Aves or the class Reptilia. In the former case one would not know whether or not the organism was homeothermal, had feathers or scales, incubated its eggs by sitting on them, had an imperfectly or perfectly four-chambered heart, etc. With minor exceptions this information is contained in the designations "avian" and "reptilian."

A further argument in favor of the static base is the relatively high repeatability and communicability of the results obtained. It is very likely that within the next decade methods will be developed which will produce nearly identical static classifications when used on different sets of characters (e.g., on, say, 150 random larval and 150 random adult characters of a group of insects). In addition, when discussing the relationship between two entities, a statement of correlation level is more concise and meaningful than a vague statement such as "X and Y appear to have a relatively recent common ancestor."

There is always the third alternative: that of basing a classification on both types of relationship together. That a mixture of two non-compatible systems is less desirable than either of them alone is evident.

Michener discusses at some length the question of what weight to give to group size (i.e., the number of entities included in a taxon) when developing a formal classification. He states "*Archaeopteryx* would be regarded as a peculiar feathered reptile had not the large group of birds evolved" and "if there were but one genus of pollen-collecting sphecoid wasps they would be considered just that. It is only because there are hundreds of genera and thousands of species that the bees are customarily placed in a superfamily separate from that of the sphecoid wasps." Michener feels that subjective decisions should be made on the size of taxa; that overly large and monotypic taxa are in general to be avoided by subjective splitting and lumping. This view is shared by many other highly competent systematists.

If we are ever to put systematics on a reasonable plane of objectivity, such manipulation for the sake of convenience must be avoided. The chemist does not lump rare elements in the periodic table with common ones of similar property for the sake of convenience, nor does he consider isotopes of the common elements to be elements themselves. While systematics is a long way from the objectivity and precision of certain physical sciences there is no reason for not striving towards this goal. Group size should only be considered in selecting the correlational level on a diagram of relationships at which the vertical lines will be considered genus stems (or family, or subfamily stems, etc.). This correlational line must be straight—to curve it down to "let in" a monotypic entity, or up to divide a large group removes much of the meaning from the system. However, the level of the line can often be adjusted in order to take into consideration group size (see Ehrlich, 1958). Obviously the correlational level in many cases can only be kept constant within the next highest taxon (correlations among bird families are not necessarily equivalent to those among beetle

families), but in many others (especially those dealing with lower categories such as subgenera and genera) this "principle of equivalence" can be employed across a relatively broad spectrum of forms.

In the case of *Archeopteryx* as the only known bird, the genus would quite properly be considered reptilian by both the WVG method and conventional systematic technique. Conversely, if the only known bird was *Turdus migratorius* both methods would probably place it in a separate class. Similarly, if the only known pollen-collecting wasp was the primitive colletid bee *Hylaeus,* then doubtless it would be lumped with the sphecoids. On the contrary, if it was the honey bee (*Apis mellifera*), it would almost surely be placed in a separate superfamily. Group size also enters into the WVG method because of the averaging of the correlation coefficients. *Hylaeus* would surely show a relatively high correlation with the sphecoid average, *Apis,* a low one. Both of them contribute to the apoid average, which, along with the sphecoid average, determines the level at which the groups are correlated.

A final problem mentioned by Michener deserves comment. This is the not infrequent situation of long series of forms separated by rather even gaps, or of connecting links between groups. These difficult situations can often be satisfactorily resolved by applying what might be called the static equivalent of the monophyletic ideal: every member of a taxon should have a closer static relationship with its nearest relative within the taxon than with any member of any other taxon. This criterion is satisfied by the WVG procedure and covers the dilemma which is diagrammed by Michener in his Fig. 5.

The Quantitative Methodology

Inger strongly attacks the WVG approach as a "typological method." The central theme of his argument is that because the "biological significance" of the individual characters is not considered (i.e., the characters are not weighted), the WVG method does not make use of the knowledge of genetics, ecology, embryology, etc., which is available for some groups. He outlines a method of establishing genera on the basis of adaptive trends.

Inger objects to the assumption of Michener and Sokal that the greater the phenotypic resemblance the greater the genetic resemblance! Until we are able to study the genotype directly as a matter of course, in the vast majority of cases there is no other possible operational assumption than that phenotypic similarity implies genetic similarity. He further refers to the "old idea (of genetics) that like begets like." It is hardly necessary to point out that in spite of tremendous recent advances, this principle remains an axiom of genetics.

Let us consider, however, Inger's more serious criticisms. He states (p. 372) "No matter how objective the calculation of the correlations may be, the Michener-Sokal technique rests on a subjective base and therefore has no advantage over the more traditional taxonomic approaches in this regard." If we assume that the choice and coding of the characters in the WVG study was entirely subjective (and this is *not* the case), does it follow that a system of relationships based on an objective (correlational) analysis of these characters is no more objective than a system based on the usual subjective-objective analysis of classical taxonomy? The answer would only be "yes" if the investigator choosing the characters were able to bias consciously the result by his selection. Various systematists (oral communication) have asked me whether it was true that Michener could have controlled the result of the WVG analysis by judicious selection of characters. The answer is "no." To anyone familiar with the intricacies of a 97 x 97 correlation matrix based on 122 characters, the idea of consciously producing a desired diagram of relationships by selection of characters (before

the correlational study has been done) is absurd.

Concerning the matter of subjectivity in selection of the characters, Michener and Sokal point out that practically all the characters previously used in the classification of the group were employed (the reader is referred to their discussion for details of why some characters were excluded). This is certainly a less subjective procedure than deciding which few of a spectrum of characters are "significant" (or represent an important adaptive complex) and basing a classification on these characters alone.

The criticism that it is subjective to divide continuous phenomena into arbitrary states (a standard statistical procedure) is unjustified. Variations in this coding would, in general, have no appreciable effect on the correlation coefficients. It might be pointed out that many apparently discrete characters doubtless have essentially continuous genetic bases (e.g., fecundity, thermal death point). Therefore in segmenting the character continuum one is merely doing artificially what is often done naturally.

Inger strongly objects to Michener and Sokal's avoidance of character weighting. However, as yet no suitable suggestion for objectively weighting characters has been made. When such a method is developed the WVG analysis can be redone using the weighted characters. It seems unlikely that the results will differ greatly from those achieved by the unweighted analysis. The WVG results were amazingly similar to those achieved by Michener by conventional taxonomic analysis of the group (including weighting). The reasons are fairly clear. The correlations are based on so many characters that they would be essentially unaffected by all but the heaviest weighting. This is a simple mathematical fact, easily verifiable by anyone with access to a desk calculator. In addition, by Inger's definition, there is some weighting in the WVG analysis. In the case of coat color vs. dentition in carnivores, the more important character (according to Inger) is dentition. In this case it would be represented in the study by numerous characters such as the jaw musculature, the form of the mandible, the shape of the skull, etc., as well as by the dentition characters themselves. The coat color would, in all likelihood, be represented as a single character.

It is my opinion that in the long run character weighting, with the possible exception of *a posteriori* weighting for conservatism, will never be generally employed in the WVG method. For reasons mentioned above it becomes trivial when sufficient characters are studied. In addition, the "importance" of a character in many cases will be too complex to evaluate as a single weight. Which among the following characters is of greatest importance to *Drosophila:* fecundity, pupation site, DDT resistance, cold hardiness, eye color, length of larval period, or wing length? This question cannot be answered without information on numerous variables, many of which change radically with time and from species to species. Thus to employ such judgments in evaluating relationships would seem unwise.

Evolutionists are vitally interested in the study of adaptation and the elucidation of phylogenies. However, knowledge of one or two adaptive trends will not replace a relatively thorough sampling of the genotype (through the phenotype) in determining the evolutionary distance (rate$\times$time) between two entities. The pitfalls of convergence are all too common when using adaptive trends as a basis for classification in well-worked groups; they are virtually unavoidable when using these methods on poorly known groups. In contrast the WVG method all but eliminates this problem.

In summary the WVG method, properly employed, provides the most objective method yet devised for obtaining the static relationships among organisms. Since these relationships are at least as important as the phyletic relationships, it

is suggested that because of their many advantages they be selected as the basis for formal classification.

REFERENCES

BIGELOW, R. S. 1956. Monophyletic classification and evolution. *Syst. Zool., 5*:145–146.

EHRLICH, P. R. 1958. The higher systematics of the butterflies. *Lepid. News, 11*:103–106.

INGER, R. F. 1958. Comments on the definition of genera. *Evolution, 12*:370–384.

MICHENER, C. D. 1957. Some bases for higher categories in classification. *Syst. Zool. 6*: 160–173.

MICHENER, C. D. and SOKAL, R. R. 1957. A quantitative approach to a problem in classification. *Evolution, 11*:130–162.

SNEATH, P. H. A. 1957*a*. Some thoughts on bacterial classification. *Jour. General Microbiol., 17*:184–200.

——— 1957*b*. The application of computers to taxonomy. *Jour. General Microbiol., 17*: 201–226.

SOKAL, R. R. and MICHENER, C. D. 1958. A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull., 38*: 1409–1438.

PAUL R. EHRLICH

Department of Biological Sciences
Stanford University, California

Similarity and Recency of Common Ancestry

In a recent paper, Bigelow (1958) has seriously questioned the validity of one of the basic principles of the evolutionary systematist, namely the correspondence between degree of similarity of organisms and their recency of common ancestry. He quite properly emphasizes that parallel evolution and disparities in evolutionary rates may lead one to draw erroneous conclusions as to the recency of common ancestry from the degree of similarity. That this may, indeed, occur has been recognized for some time by most paleontologists. Among neontologists, however, there has sometimes been a disturbing lack of appreciation of the time element and factors intimately associated with it. Bigelow has performed an important service in relating these factors to the general principle. He concludes, however, that the frequency of these "disturbing" factors may be such as to completely negate the concept as a general principle. It is with this premise that I heartily disagree, and to it that the present remarks are directed.

That there is a very significant degree of cause-and-effect association between homologous (or, by inference, genetic) similarity and recency of common ancestry is widely accepted by systematists. It may, in fact, be considered one of the axioms of the science. This status does not preclude periodic reevaluation of its validity; in fact, it should demand it. No attempt will be made here to defend the concept as a "sacred cow." Some theoretical considerations will be explored initially after which the nature of the direct evidence will be briefly examined.

With respect to the relationship between degree of homologous similarity and recency of ancestral continuity, the following hypotheses may be considered:

(1) The two variates exhibit a significant (but less than perfect) degree of direct association or proportionality.

(2) There is a random association between the two; i.e., no information concerning one may be inferred from knowledge of the other.

(3) There is significant inverse association; i.e., greater degree of similarity is usually associated with least recent common ancestry.

Hypothesis one is the generally accepted relationship. A considerable differential in evolutionary rates in given instances is not incompatible with this hypothesis. Hypothesis two is that suggested by Bigelow as very likely to be true. It is interesting to note that this relationship would follow as a necessary consequence of special creation but is, of course, also theoretically compatible with evolution. No one has, at least to my

knowledge, seriously proposed the third as a general principle. Although each hypothesis could be true as regards a limited area of the organic world, they are mutually exclusive as general principles.

The validity of any scientific principle is measured in terms of the frequency with which it leads to verifiable predictions. Thus, we are not concerned with certainty, or the lack of it, but with the probability that an hypothesis is true. It is readily apparent with respect to the relationship in question that this probability is a function of the rank of the taxa within which subunits are to be compared. At the kingdom level, for example, if we assume that each of the one million species of animals has a common ancestry later in time with another animal species than it has with any species of plant, we shall make very few errors. The chance of being wrong is not equal for all groups, being considerably greater for the chlorophyll-bearing flagellates than for, say, the arthropods. If we compare three subunits (e.g., genera) within two phyla or within two classes or orders, etc., we shall be right in the overwhelming majority of cases, but with decreasing frequency as the scope of the taxa narrows. If comparisons are made between taxa, as such, without reference to the included subunits, hypothesis one will be verified in most instances in which it can be adequately tested. Difficulties may arise, however, particularly among the lower invertebrates, with respect to the initial step, i.e., the satisfactory determination of the relative degree of similarity among the several groups to be compared. Failing this, the hypothesis cannot be formulated in concrete terms and will, therefore, be irrelevant. Arrangement according to relative similarity of some of the classes and orders of protozoans, coelenterates, and flatworms are cases in point.

The probability that hypothesis one will be true in a given instance is also a function of the magnitude of the difference in lengths of time that groups have shared a common ancestry. If A and B shared a common phyletic line from the origin of life to the Pleistocene and C was separated from this lineage in the Devonian, basic similarity will reflect the differential in common ancestry almost invariably. If C was separated in the late Pliocene, the hypothesis will be true less frequently. It follows that where the chances of error are the greatest, the seriousness of the error is at a minimum. Bigelow suggests that, subsequent to the cockroach-grasshopper dichotomy, another line could have arisen from the roaches in the Carboniferous which also became grasshoppers. This is possible, though improbable in the absence of cogent direct evidence, and its improbability increases rapidly as we approach the Recent.

Perhaps an analogy concerned with the age-size relationship during ontogeny may be helpful at this point. If we compare 20-gram rats with those of the 200-gram class, deductions as to relative age will rarely be in error. As the weight differential is narrowed, the chance of being wrong gradually increases. When the size interval is reduced to one gram, the incidence of incorrect inferences will be high. That this is so does not, of course, negate the age-size correlation as a general principle.

There are at least three lines of direct evidence which may be adduced in support of the generally accepted hypothesis. First of all we have the facts related to the nature of rate of change in organisms. A basic consideration is the frequency of mutation. Although there is a great deal of variation in mutation rates, they do not vary at random in the sense that of N possible rates, the probability of occurrence of each is 1/N. Most well established rates are at or near a modal class of 10^{-5} or 10^{-6} per locus per gamete. The same situation also pertains to selection whose efficacy as regards rate of change is well recognized. Although selection pressures may vary tremendously, their average ef-

fect must be approximately the same order of magnitude within most groups most of the time. Studies of rates of evolutionary change which, to a large extent, reflect mutation and selection pressures, corroborate this view. Recognizing that rates are by no means constant, it does not follow that they must necessarily exhibit a random distribution. Quantitative studies of related lineages of familial or higher rank consistently show a strong tendency for rates to cluster around a modal value (Simpson, 1953; Haldane, 1949; Bader, 1955). Simpson, who has carried out both intensive and extensive studies of evolutionary rates, states (*op. cit.*, p. 317):

"The peakedness of these distributions shows that among related lineages, most of them tend to evolve at about the same rate. In extinct pelecypod genera about a third, in extinct carnivore genera about half, and in extinct centric diatom species about three-fourths evolved at rates included in only one-tenth of the whole range of variation in rates. These concrete data confirm the vague and subjective estimation of many paleontologists that each group of organisms does have a characteristic rate of evolution approximated by most lineages in the group."

As regards parallel evolution, of which there has been increasing recognition in recent years, one can only speculate as to even the order of magnitude of its general incidence. The actual frequency of the phenomenon will, undoubtedly, be found to vary extensively from group to group. The number of well-documented cases in which alternative explanations can, with confidence, be ruled out, remains relatively small. We have certainly not approached the point at which parallelism must, in general, be assumed in the absence of evidence to the contrary.

The second line of evidence is derived from extant infraspecific assemblages down to, and including, the deme or clan. The differential with respect to recency of common ancestry is small; it is under such circumstances that hypothesis one may be most unreliable. In spite of this, when we consider the various breeds and strains of domestic and laboratory animals, or the races of man, the reliability of the association as a general rule is apparent. At the clan or even the parent-sib level, it is well established that there is a significant departure from randomness.

Finally, and perhaps most importantly, we have the evidence from groups which possess a good historical record and which will, therefore, be invaluable in testing the hypothesis. An example will be taken from the Class Mammalia, which has, in general, an excellent fossil record. If we compare, say, the horse, zebra, tapir, shrew, and opossum, arrangement according to degree of similarity will be found to correspond very well with that based on paleontologically established recency of common ancestry. Hundreds of similar mammalian examples could be given. With the general reliability of the association well established, a mammalian systematist may, with some confidence, make deductions as regards the phylogeny of groups with poor fossil records, e.g., the monotremes and Australian marsupials. Such unverified predictions do not, as Bigelow points out, give additional support to the hypothesis in question. However, in the lineages with the best documentation, e.g., the Equidae, they are not usual or necessary. Another manifestation of the correspondence is the general agreement of classifications based on living as contrasted to fossil mammals. The classification of recent mammals would not be radically different in its major outlines, or in much of its detail, had not a single fossil of the class been discovered. This would be less true of groups such as the amphibians and reptiles, most of whose representatives are now extinct.

It is generally recognized by paleontologists that many taxa of specific or higher rank may appear rather abruptly in the record. Bigelow quotes Simpson (*op. cit.*, p. 360) to this effect and, then, jumps to the conclusion that the explanation must

be sought in terms of saltation or very rapid evolution. The most obvious and generally accepted interpretation of most of these occurrences is the imperfection of the record. (This was discussed by Simpson a little later on the same page from which the quotation was taken.) Even if the surmise advocated by Bigelow were true in most instances, so-called rapid rates would be commonplace and would not, therefore, materially alter the general nature of the relationship in question.

In conclusion, it should be emphasized that none of the foregoing remarks are intended to cast any doubt on the ability of differential rates of change and parallel evolution to obscure the basic relationship in specific instances. That all students of systematics should be cognizant of these factors is beyond dispute. This is most particularly true for those who draw phylogenetic conclusions without fossil evidence from similarities of taxa of lower rank. That these factors invalidate the generally accepted relationship as a general principle is, however, an unwarranted conclusion.

REFERENCES

BADER, R. S. 1955. Variability and evolutionary rate in the oreodonts. *Evolution, 9*:119–140.

BIGELOW, R. S. 1958. Classification and phylogeny. *Syst. Zool., 7*:49–59.

HALDANE, J. B. S. 1949. Suggestions as to quantitative measurement of rates of evolution. *Evolution, 3*:51–56.

SIMPSON, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.

ROBERT S. BADER

Department of Zoology,
University of Illinois,
Urbana, Illinois

Index for Volume 7 (1958)

BADER, R. S. Similarity and recency of common ancestry 184

BARNARD, J. L. The question of decline in systematic activity, measured in the marine Amphipoda 123

BIGELOW, R. S. Classification and phylogeny 49

BOUSFIELD, E. L. Book review: Index to the families, genera, and species of the gammaridean Amphipoda (Crustacea) 136

BROWN, W. L., JR. General adaptation and evolution 157

BURCH, J. B., and THOMPSON, F. G. Taxonomic characters and infraspecific variation in mollusks 48

CHRISTIANSEN, K. Geographic variation and the subspecies concept in the collembolan *Entomobryoides guthriei* 8

EHRLICH, P. R. Problems of higher classification 180

EVANS, J. W. Character selection in systematics with special reference to the classification of leaf hoppers (Insecta, Homoptera, Cicadelloidea) 126

HAGMEIER, E. M. Inapplicability of the subspecies concept to North American marten 1

HANSON, E. D. On the origin of the Eumetazoa 16

HARTMAN, W. D. A re-examination of Bidder's classification of the Calcarea 97

HOOD, J. D. The terms tergum and sternum, tergite and sternite 131

HYMAN, L. H. In regard to nema the thread 133

KIRKEGAARD, J. B. The distribution of the Pogonophora 95

LEVINE, N. D. Uniform endings for the names of higher taxa 134

LONGHURST, A. R. Abnormal variation in the Notostraca 84

MULLER, S. W. Korobkov's proposal of a new morphologic entity, *forma accommodata*, in Mollusca 89

PIMENTEL, R. A. Taxonomic methods, their bearing on speciation 139

REISH, D. L. An analysis of a sample of systematic literature, 1758 to 1954 174

SMITH, H. M. The synthetic natural populational species in biology 116

SMITH, R. I. On reproductive pattern as a specific characteristic among nereid polychaetes 60

STARRETT, A. What *is* the subspecies problem? 111

TUCKER, R. Taxonomy of the salivary glands of vertebrates 74

WOOD, A. E. Are there rodent suborders? 169

YOUNG, D. A., JR. On lectotype proposals 120

... 184
the
... 123
.... 49
the
.... 136
.... 157
vari-
.... 48
lem-
.... 8
.... 180
the
.... 126
rican
.... 1
..... 16
a.... 97
..... 131
..... 133
..... 95
..... 134
..... 84
mmo-
..... 89
..... 139
..... 174
..... 116
nereid
..... 60
..... 111
..... 74
..... 169
..... 120

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Manuscripts must be mailed flat, not folded or rolled. They must be typed double-spaced on standard typewriter paper, with ample margins on all four sides. Double-spacing applies to all parts of the manuscript—footnotes, legends of figures, literature list, tables, etc. Footnotes are numbered consecutively and may be placed in the text between horizontal lines or listed on a separate page. Literature list will be headed REFERENCES and will follow style in recent issues of the journal, thus: name of author, year, exact title, journal name abbreviated, volume number, first and last pages. Journal abbreviations may follow usage in *Biological Abstracts*. Avoid excessive abbreviation as in the *World List*, not recommended. Journal names consisting of a single word (*Science, Evolution, Genetics,* etc.) are written out in full, as are also names of unusual or rare journals. Geographic names (*London, California*) are not abbreviated. Number of issue of a journal is not wanted unless such issues are repaged. Number of figures and plates may be omitted. Books are referred to as follows: author, year, exact title, name of publisher, location of publisher. Tables are typed on separate sheets placed in correct sequence in the text. Tables are expensive to set and should be limited to the strictly necessary. Avoid vertical lines. Illustrations should preferably be prepared for reproduction as line cuts, but illustrations requiring half-tone reproduction are acceptable. Illustrations are usually made larger than, but not more than twice as large as, their eventual size in the published journal. In preparing illustrations, the dimensions of the printed page (8 x 5¼ inches) should be kept in mind. Figure legends are typed on a separate page placed at the end of the manuscript. The full scientific name of an animal, including the author and year, must be given the first time the animal is mentioned.

Authors receive galley proof accompanied by a reprint order and are reminded that changes in proof are expensive. They should not attempt to rewrite the article on the galley proof. The cost of alterations made in proof will be charged to the author if it exceeds ten per cent of the cost of composition. Authors should inform the editor whether or not they wish the original illustrations returned. To avoid delay authors with articles in press should keep the editor informed of any permanent or temporary change in address.